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BULLETIN OF THE TORREY BOTANICAL CLUB
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A NEMATODE-DESTROYING PHYCOMYCETE FORMING IMMOTILE SPORES IN AERIAL EVACUATION TUBES

CHARLES DRECHSLER[1]

A new nematode-destroying fungus which offers unusual features both in its parasitic development and in its asexual reproduction was obtained from partly decomposed leaves of the red maple (*Acer rubrum* L.) that were taken, on August 27, 1944, from a thick mat of decaying foliage bordering a pond several miles north of Georgetown, Delaware. At the time the collection was made, the mat, about 20 cm. in depth, held only such moisture as had been absorbed from the ground, but its low position must have exposed it to flooding whenever the pond was swollen by rain. In accordance with routine procedure small quantities of the friable detritus were added to maize-meal-agar plate cultures already thoroughly overgrown with either *Pythium ultimum* Trow or *P. undulatum* Petersen sensu Dissmann. During the ensuing two weeks various forms of animal life, including nematodes in large part referable to the genera *Acrobeloides, Aphelenchoides, Plectus,* and *Rhabditis,* multiplied freely in the cultures. The abundant eelworms soon were attacked by several widely distributed parasitic and predaceous hyphomycetes such as *Arthrobotrys oligospora* Fres. and *Harposporium anguillulae* Lohde. Somewhat later, 19 days after the plantings had been made, the new parasitic fungus was first observed in small quantity in one of the plate cultures. Afterward it came to light also in more than a dozen other cultures of the same series. In all the cultures it attacked only a single species of eelworm which Dr. G. Steiner has kindly identified as a species of *Acrobeloides* clearly distinct though not widely different from *A. bütschlii* (De Man) Thorne so prevalent in the vicinity of Washington, D. C.

The attack of the fungus begins with the adhesion of one or more of its conidia to the integument of a susceptible animal (fig. 1, a). Each of the adhering conidia puts forth a germ tube which maintains a width of approximately 1 μ in penetrating the host cuticle and in passing through the muscular body wall. When the body cavity is reached the germ tube immediately widens out in the manner of a pestle (fig. 1, b). The entire protoplasmic contents of the conidium then migrate into the expanded tip (fig. 3, a, b) to form a globose bud which soon detaches itself as a young thallus ready for para-

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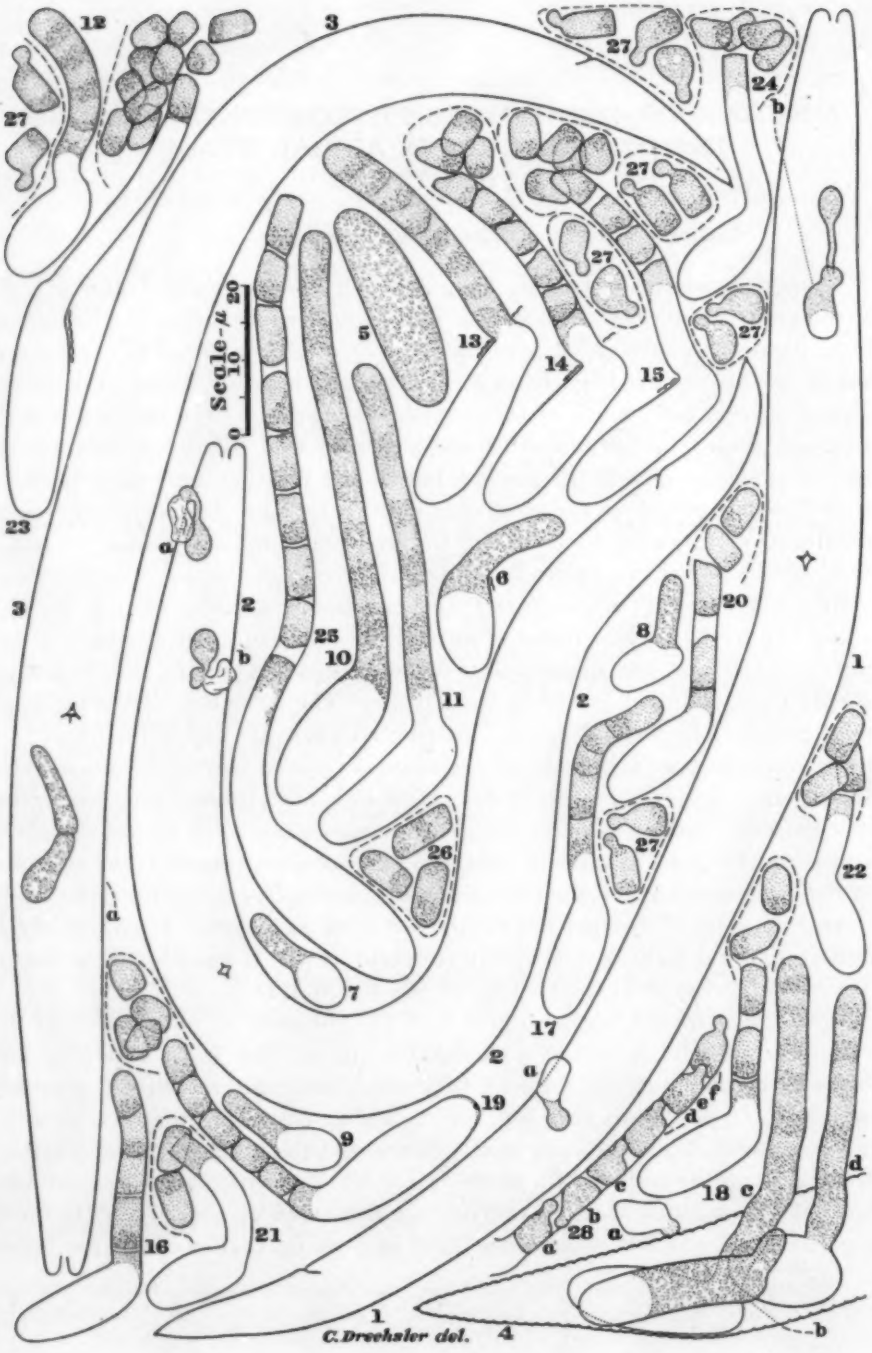
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sitic growth; the empty infection tube thereupon being nearly always lost to view, though the empty conidial envelope may often be seen affixed in much later stages (figs. 4, a; 33, a, b, c).

The young thallus, loose within the body cavity of the host, gradually elongates despite the frequently rather active bustling to which it is subjected by the animal's undiminished locomotion. When its length has come to exceed its width 3 or 4 or 5 times a cross wall appears in the middle, dividing it into 2 subequal cells (fig. 29) only slightly larger than the parent cell was originally. The 2 daughter cells grow somewhat in size as they become rounded off at the median septum in preparing for disjunction (figs. 2, a; 30), an event apparently hastened a little by the repeated flexural strains resulting from active movements of the eelworm. The separated unicellular bodies then gradually elongate and in due course, like their parent, undergo median partitioning and disjunction (fig. 31). Before long, on continued repetition of the same developmental sequence, a dozen thallodic cells are to be seen jostled about in loose disorder (fig. 32). Far from affecting these cells unfavorably, the jostling seems actually to help them in extending their distribution lengthwise within the animal, and more particularly in pushing them slowly through the narrowed portion of the body cavity where the

Explanation of figures 1–28

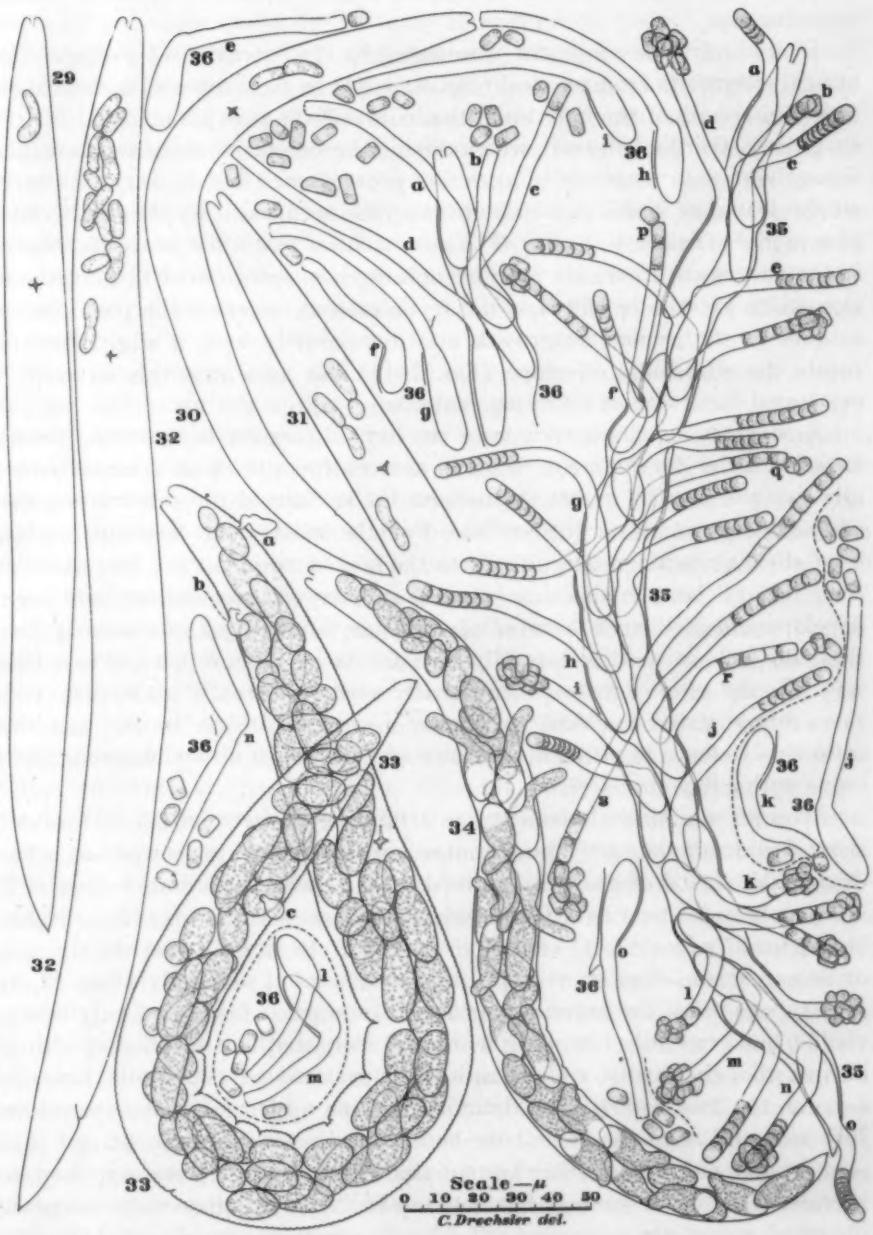
Gonimochaete horridula, drawn to a uniform magnification with the aid of a camera lucida; ×1000. FIG. 1. Small specimen of *Acrobeloides* sp. in early stage of infection from 2 adhering conidia, a and b; the infection tube from b is extended at an angle affording a good view. FIG. 2. Small specimen of *Acrobeloides* sp. with 2 adhering conidia, a and b, that have yielded their protoplasmic contents to the terminal enlargements within the body cavity of the host. FIG. 3. Small specimen of *Acrobeloides* sp. containing in its body cavity a uniseptate thallus whose 2 cells are about to become disjointed. FIG. 4. Posterior portion of infected specimen of *Acrobeloides* sp. with an empty spore envelope, a, adhering to it externally, and with 3 thallodic cells contained inside of it; one of the cells, b, having just begun to put forth a hyphal outgrowth, the other 2 cells, c and d, having each completed production of a hyphal outgrowth. FIG. 5. Large thallodic cell. FIG. 6. Thallodic cell in course of extending a hyphal outgrowth. FIGS. 7–9. Thallodic cells with fully extended hyphal outgrowths. FIGS. 10–13. Thallodic cells with hyphal outgrowths whose contents are arranged in alternate granular and homogeneous layers, indicating cleavage into spores. FIG. 14. Same sporangium as in figure 13, but after 3 spores have been liberated in a first discharge. FIG. 15. Same sporangium, again, as in figure 13, but after 2 more spores have been liberated by a second discharge. FIGS. 16, 17. Thallodic cells with sporangial hyphae ready for discharge of spores. FIGS. 18–22. Thallodic cells with sporangial hyphae, after discharge of a few spores from each. FIG. 23. Large thallodic cell whose sporangial hypha has liberated 10 spores, 1 spore being still attached to the closed end of the persistent basal part of tubular membrane; the proximal end of each spore is distinguished internally by an accumulation of granules. FIG. 24. Rather small thallodic cell whose sporangial hypha retains some protoplasm, after it has discharged 4 spores. FIG. 25. Large thallodic cell whose sporangial hypha retains some protoplasm and 8 spores, following the liberation of one or more spores at the tip. FIG. 26. Liberated spores of more than average size. FIG. 27. Spores that after their liberation have each put forth an adhesive protuberance. FIG. 28. Spores *a–f*, each of which has put forth an adhesive protuberance while still inside the envelope of the sporangial hypha.

oesophageal bulb occupies nearly the entire lumen of the body wall. Owing to the greater frequency of anterior infections, the portion of body cavity forward of the bulb is usually occupied earlier than the posterior portion. However, development of the fungus around the yielding intestine would seem to proceed more rapidly than about the resistant oesophagus, for when the thallodic cells have attained their definitive number they are usually found distributed rather evenly from one end of the animal to the other. As might be expected from the manner of multiplication, the definitive number of thallodic cells—commonly between 15 and 80—is little influenced by the number of original infections, but is determined primarily by the size of the individual animal host.

After their multiplication has ceased the thallodic cells grow in size without undergoing any pronounced change in their elongate ellipsoidal or occasionally subspherical shape. They increasingly choke the body cavity, yet for a protracted period the animal continues to move about with little show of distress or physical weakness. In many instances its behavior remains seemingly normal even after the total volume of the fungus cells appears approximately equal to the combined volume of its musculature and organs. Somewhat later, however, its locomotion slows down gradually and stops, disablement here being accompanied by incipient evanescence of the peripheral musculature. Usually the body wall backward from the oesophageal bulb begins to fade from view somewhat earlier than the anterior portion of the wall. In all cases, certainly, the oesophagus and bulb resist dissolution far better than the intestine or, indeed, than any other fleshy part. Thus, in the specimen shown in figure 33 the oesophagus and bulb, though crowded from their normal position, could still be clearly distinguished at a stage when all other contents had been reduced to diaphanous vestiges. Eventually these durable muscular parts also suffer obliteration in some degree, even if in more than a few instances they remain discernible when the thallodic cells

Explanation of figures 29–36

Gonimochaete horridula, drawn to a uniform magnification with the aid of a camera lucida; ×500. FIGS. 29, 30. Specimens of *Acrobeloides* sp., each infected by a single uniseptate thallus. FIG. 31. Anterior portion of a specimen of *Acrobeloides* sp. infected with 3 uniseptate thallodic bodies. FIG. 32. Specimen of *Acrobeloides* sp. infected with 12 thallodic bodies, some continuous, others uniseptate. FIG. 33. Large specimen of *Acrobeloides* sp. killed by parasite, following infection from 3 conidia, a–c, and development of 76 thallodic cells in its body cavity. FIG. 34. Specimen of *Acrobeloides* sp. killed and expropriated of contents through development of 40 thallodic bodies of the parasite; many of the bodies have begun to extend sporangial hyphae. FIG. 35. Integument of a specimen of *Acrobeloides* sp. occupied by 34 empty thallodic cells whose contents have been utilized for production of spores; most of the sporangial hyphae, including the 15 designated by the letters from a to o are shown in ascending posture; 4 others, p, q, r, and s, being shown in submerged positions. FIG. 36. Fifteen aerial sporangial hyphae, a–o, flattened down in a moist preparation under a cover glass; these being the same hyphae as those designated by corresponding letters in the preceding figure.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have manifestly concluded their vegetative growth, to proceed with asexual reproduction.

Reproductive development is initiated by the extension of a single stout hyphal outgrowth from one end (figs. 4, b; 34) or from a position close to one end (fig. 4, c, d) of the individual thallodic cell. To provide material for this outgrowth, the thallodic cell, which during the vegetative stage remains filled throughout with dispersedly granular protoplasm (figs. 5, 33), is progressively cleared of visible contents at the opposite end as if by the enlargement of a vacuole (figs. 4, b; 6; 34). The movement of materials proceeds steadily as the outgrowth forces its way through the host integument to continue its elongation externally (fig. 4, c, d). In occasional instances the protoplasmic column in the hyphal outgrowth may temporarily keep a slight foothold inside the ellipsoidal envelope (figs. 7–10) but as a rule this envelope is evacuated forthwith of all living contents.

A conspicuous characteristic of the hyphal element is its strong preference for aerial development. Since in agar cultures the host animals habitually live and feed on rather than under the surface of the substratum, they ordinarily succumb on the surface. For the most part, consequently, the hyphal elements after emerging from the host integument are free to follow their natural bent in choosing between submerged, procumbent, and aerial development. Although some of the hyphae, especially those arising from thallodic cells covered or laterally hemmed in by their fellows, thrust their way into the agar or grow procumbently over it, virtually all hyphae from favorably situated thallodic cells grow ascendingly into the air, and thus collectively offer a bristling appearance (fig. 35) when viewed under a microscope with a dry objective.

Soon after a hyphal element has attained definitive length its contents show significant changes. The granular constituents of its protoplasm, which during the period of growth remained rather evenly distributed (figs. 6, 7) are now brought together at intervals in a series of transverse clumps numbering usually fom 2 to 11 (figs. 4, c, d; 10–12). Beginning near the tip, lines of demarcation, often curving downward somewhat obliquely (figs. 13, 16, 17), appear below the individual granular clumps, at first being only faintly visible, but gradually becoming more and more distinct. Suddenly, with an abrupt though hardly violent upward movement of the whole stratified column, the 2 or 3 or 4 parts delimited by the uppermost lines are pushed forward; and as at the same time both their linear arrangement and their connections with one another become disrupted through buckling, they are revealed as discrete spores (figs. 14, 18, 19–22, 24). Apparently the newly liberated spores are somewhat adhesive, for in instances of aerial development they flip backward and remain clinging to the shortened hypha in an irregular cluster. The portions of protoplasm still in the hypha then undergo

further gradual individualization, and after a period of perhaps 15 to 30 minutes 2 or 3 more spores are abruptly though gently pushed forward (fig. 15). Many of the shorter hyphal outgrowths discharge only once or twice, but the longer hyphae originating from the more voluminous thallodic cells (fig. 23) may give 3 or 4 puffs; each successive increment of spores, in the case of aerial hyphae, becoming agglutinated to those already clustered at the tip. Sometimes the lowermost spore remains in place, attached to the empty hyphal membrane (figs. 23; 36, c). The occasional instances where several spores or, at times, nearly all of the spores remain in alignment (fig. 25) until the enveloping hyphal membrane disintegrates must be held to have their explanation in partial or complete failure of the discharge mechanism.

Thus, in a general way, the hyphal outgrowth functions both as a sporangium and as an evacuation tube. Its operation in the latter capacity, however, shows marked peculiarity not merely in the gentle, intermittent propulsion of the spores, but also, and more especially, in a progressive wastage of the distal portion of the hyphal membrane, through which the original length of the membrane may be reduced by more than a half. It is not easily determined just how this wastage is accomplished. As the outgrowth before discharge reveals no conspicuous modification of its apex, there is reason to believe that the initial rupture of the membrane is not usually at the tip, but more often between the apical and the penultimate spore; wherefore it seems probable that in the very beginning the tubular envelope is shortened through removal of a distal portion adnate to the apical spore. If the first pufflike discharge leaves unoccupied a portion of hyphal envelope at the new apex, this ordinarily disintegrates quickly, thereby further shortening the tube. Similar loss of membrane takes place with each succeeding puff, until discharge is completed. Another peculiarity then becomes manifest in that the abbreviated hyphal membrane is usually not left open at the tip, like evacuation tubes generally, but is closed securely by a terminal wall (fig. 36, a–o). Where deposition of such a wall is omitted, as is frequently the case in specimens submerged in an agar mount prepared for study under the microscope, the hyphal membrane and the empty envelope of the thallodic cell promptly collapse and are soon lost to view. Where, however, the tip of an ascending aerial element has been closed, the entire membranous container, like an ancient skin bottle, retains its turgor and shape for a prolonged period, with the result that the shortened hyphal element continues to project upward, bearing aloft its cluster of spores. In fine, through closure of its tip the hyphal element that previously had served as sporangium and evacuation tube is enabled to operate as a sporophore. Occasionally hyphal outgrowths in submerged or procumbent positions likewise become sealed distally, though here it is not evident that any purpose could be fulfilled by the continuing turgor of the evacuated receptacle.

When newly liberated the spores (figs. 14, 15, 18–20, 22–24, 26; 36, a–o) are of a generally cylindrical shape. In the shorter specimens the length scarcely exceeds the width, while in the longer specimens it may slightly exceed twice the width. Most of the spores are somewhat unsymmetrically rounded or obliquely truncate at the ends; those formed terminally being, as a rule, quite readily distinguishable from their fellows since they regularly retain the symmetrically rounded apical contour of the parent hyphal outgrowth. All of them lack locomotor organs of any kind, and consequently are completely immotile. When brought into contact with a moist substratum they undergo incipient germination, each giving rise, often obliquely from one end, to a small excrescence (fig. 27) with a profile suggestive of the protruded head of a turtle. Judging from instances where frustration of the discharge mechanism has left the spores within the envelope of the parent hypha (fig. 28), the excrescence more often arises from the distal end (fig. 28, a, c–f) than from the proximal end (fig. 28, b). As might be surmised from analogy with similar development in other fungi parasitic on free-living terricolous nematodes, the germ protuberance is strongly adhesive and serves an important function in attaching the spore securely to the integument of a prospective host.

The vegetative development of the fungus can be followed no less clearly than its asexual reproduction, owing to the fortunate circumstance that animals infected by it suffer expropriation of their contents without showing the globuliferous degeneration through which the invasion of nematodes by nearly all parasitic and predaceous forms is often obscured to a troublesome degree. While the determination of its morphology and development in most particulars thus offers little difficulty, the taxonomic relationships of the fungus are not as obvious as might be desired. The general resemblance of its thallodic cells to the thalli of various zoospore-producing phycomycetes that have been made known as nematode parasites—*Chytridium endogenum* Braun (41), *Chytridium zooticum* Braun (2), *Catenaria anguillulae* Sorok. (7, 41), *Achlyogeton entophytum* Schenk (40), and *Myzocytium vermicolum* (Zopf) Fischer (11, p. 75; 44) may be cited as examples—immediately suggests that the immotile spores could well have been derived through evolutionary processes from some type of motile zoospore. Loss of motility in zoospores might, indeed, readily be associated with adaptation to parasitism on free-living nematodes, since the very active locomotion of these animals in itself provides adequate opportunity for encounter between host and parasite, thereby making independent movement of the parasite unnecessary, while at the same time encouraging strong adhesiveness as a feature of primary importance. The immotile spores of the fungus I have described (10) as *Haptoglossa heterospora* can be credibly interpreted as being homologous with zoospores not only by reason of their original subspherical shape

and their violent discharge from massive sporangia formed from endoparasitic thalli, but by reason further of the persuasive parallelism that is evident when their emission of individual glossoid infective bodies is compared with the emission of a second zoospore stage in diplanetic development of the type familiar in *Achlya* and *Aphanomyces*. However the immotile spores of the Delaware fungus are not typically subspherical at any time, and do not reveal anything suggestive of diplanetism or of any other developmental feature especially characteristic of zoospores. In respect to their ambiguous morphology they invite comparison with the acutely pointed tapering immotile spores of the nematode parasite *Protascus subuliformis* Dangeard (8), which in shape likewise differ very markedly from zoospores, and which in manner of germination betray no particular homologies of any kind. If Maire (29) was able, with some credibility, to interpret the tapering spores as aplanospores equivalent to zoospores, it was mainly because the morphology of the thallodic sporangium in which they were formed and the violent manner of their discharge, together with the morphology of the sexual apparatus ascribed by Maupas (30) to *P. subuliformis*, gave grounds for recognizing a possible relationship to the zoosporiferous genera *Achlyogeton* and *Myzocytium*. While such relationship might be held similarly indicated for the Delaware fungus by the multiplication and outward morphology of its thallodic cells, parallelism with zoosporiferous phycomycetes generally is not well sustained either in the behavior of its hyphal outgrowths or in the intermittent maturation and discharge of its immotile spores.

What would seem in some measure a departure from the usual course of development among zoosporiferous phycomycetes is shown by the Delaware fungus in the complete evacuation of undifferentiated materials from the thallodic cell into a hyphal outgrowth corresponding structurally to the evacuation tubes of various chytrids and oomycetes. Yet however alien such transfer of protoplasmic materials, followed by zoospore or aplanospore individualization within the filamentous element, may be to the genera *Achlyogeton*, *Myzocytium*, *Protascus*, and *Haptoglossa*, similar movement of contents occurs as a rather commonplace event in the germination of some oospores. Thus, for example, when the oospores of my *Aphanomyces camptostylus* germinate by the production of zoospores, individualization of the swarm spores often takes place wholly within the germ hypha (9, p. 340, fig. 11, J). But while the sporogenous germ hyphae produced by *Aphanomyces* oospores are habitually extended into any deposit of liquid water that may be available, the sporogenous hyphal outgrowths of the Delaware fungus reveal a strong preference for aerial development wherever their positional relationships are not too unfavorable. To this preference, which even by itself would need to be regarded as very exceptional in an evacuation tube, are added further anomalous features in the curious evanescence of the distal

portion of the hyphal membrane during spore discharge, and in the terminal closure of the empty proximal portion persisting after discharge is completed.

Most of the features that give difficulty in reckoning the Delaware fungus among the zoospore-producing phycomycetes find striking analogies in the entomophthoraceous nematode parasite I described earlier (10) as *Meristacrum asterospermum*. In one species as in the other the thallodic cells are completely evacuated of contents as the protoplasmic materials migrate into sporogenous hyphae that show a strong tendency toward aerial development. In both fungi, again, spore formation proceeds from the tip toward the base, and spore liberation is accompanied by rapid collapse and evanescence of a terminal portion of the hyphal membrane. The wall which in the Delaware fungus closes the empty portion of the sporogenous outgrowth offers good correspondence with the septum that in *M. asterospermum* proximally delimits the lowermost sporogenous hyphal segment. *M. asterospermum*, it is true, forms its immotile spores not endogenously, like the Delaware fungus, but in a typically exogenous manner by burgeoning them forth laterally from the several individual segments formed through deposition of cross-walls in the helicoid distal portion of the sporogenous hypha. Although these exogenous spores, or conidia, show unmistakable general resemblance to the much larger conidia familiar in the insectivorous Entomophthoraceae, they would seem more accurately homologous with the small secondary conidia whose production plurally from large primary conidia, following simultaneous emission of multiple sterigmata, was first made known by Costantin (5) as a distinctive feature of *Delacroixia coronata* (Cost.) Sacc. & Sydow (39, p. 457) and more recently was also observed by Couch (6) as an incidental phase in the development of his *Conidiobolus Brefeldianus*. In accordance with such homology the large conidium of *D. coronata*, and, by extension, the large conidia of the Entomophthoraceae generally, would be morphologically equivalent to the distal helicoid sporogenous portion of the hyphal element thrust into the air by the individual thallodic segment of *M. asterospermum*. Similar parallelism, but relating to endogenous immotile spores rather than to conidia, becomes evident when the Delaware fungus is compared with *Basidiobolus ranarum* Eidam: the distal sporogenous portion of the hyphal outgrowth in the former having its morphological equivalent in the large conidium of the latter; and the immotile spores of the former corresponding to the secondary bodies formed plurally, according to Levisohn's (28) account, within the large conidia of the latter after their ingestion by frogs, or often, too, on immersion in a glycerin-peptone-glucose culture solution. Levisohn discussed the endogenous bodies merely as products of multiplication, referring to them and to their development in language (Tochterzellen, Abkömmlinge, Darmform, Konidienzerfall, Hyphenzerfall, Teilung) even less connotative of homologies pertaining to reproduction

than the term "Palmellastadium" by which Raciborski (38) had earlier designated aggregations of similar bodies he found produced within mycelial segments when he grew *B. ranarum* in a culture solution containing ammonium sulphate and glucose. Nevertheless in subsequent text-books on mycology (13, p. 118, 119; 12, p. 285; 1, p. 115–117; 14, p. 147) the endogenous bodies have been interpreted as sporangiospores, and for the most part Levisohn's findings seem to be construed confidently as having established the sporangial nature of the large conidia common to nearly all known members of the Entomophthoraceae. It is not difficult to understand how an investigator dealing at first hand with *B. ranarum* might well be reluctant to use terminology distinguishing between asexual reproduction and vegetative segmentation, for in that fungus, under natural conditions, the development corresponding to the formation of endogenous spores in the hyphal outgrowths of the Delaware parasite takes place, apparently without much spatial separation, in the same milieu—the interior of the frog's alimentary tract—as the vegetative multiplication corresponding in the Delaware parasite to the repeated fission of young thallodic cells inside the body cavity of the nematode host. The circumstances making for confusion of the reproductive and vegetative stages in *B. ranarum* are wholly absent in the Delaware fungus; so that this fungus—unless the parallelisms it offers are misleading—displays advantageously what would appear to be the primal manner of asexual reproduction in the family. The difference between its method of spore formation and the method of spore formation in *M. asterospermum* seems approximately of the same sort as the difference between the types of asexual sporulation found, respectively, in *Mucor* and *Cunninghamella;* though the *Dictyuchus*-like partitioning of the sporogenous hyphal tip in *M. asterospermum* has no equivalent in *Cunninghamella* nor, for that matter, in *D. coronata* and *C. Brefeldianus.* It may be noted that the spores of *M. asterospermum* put forth no special adhesive protuberance, but become affixed to the animal host by means of adhesive material which they exude without undergoing any modification in outward shape. Again, instead of increasing numerically by repeated fission during the earlier stages of invasion, the infective cell of *M. asterospermum* grows into a stout massive hypha before division by deposition of cross walls takes place preliminary to disjunction.

If among the groups of phycomycetes mainly endoparasitic on animals and reproducing asexually by immotile aerial spores the Delaware fungus is brought into alignment with the Entomophthoraceae by virtue of its ready fissiparous multiplication, it is through this same feature of vegetative development estranged from the Zoopagaceae; since in the latter family thallodic or mycelial disjunction is wholly unknown, and apart from the septa associated with reproduction, transverse walls are laid down within thallus,

hypha, or germinating conidium solely as retaining walls to mark successive stages in the evacuation of these structures. Then, too, the contents of the disjointed vegetative cells show sharp contrast between the sappy protoplasmic matrix and the granules scattered through it in moderate numbers, whereas the denser protoplasmic matrix in the thalli and vegetative hyphae of the Zoopagaceae often obscures the granular constituents rather markedly. Although in the Delaware fungus the spores usually do not appear spatially separated from the membrane of the hyphal outgrowth within which they are formed, their visible movement upward through the lumen of the membranous envelope gives ample evidence of their endogenous origin. Among the Zoopagaceae, on the other hand, movement of spores within the membrane of a parent hyphal element has never been observed. Except for the empty membranous appendages borne on the conidia of some species, the spores throughout that family are indistinguishably fused with the membrane originally surrounding them; and after disarticulation each spore retains the adnate portion of original membrane as an integral part of its wall. Even the restricted analogy in sporulation offered by the three catenulate genera of the Zoopagaceae is absent in the five zoopagaceous forms that have so far been described as parasitic or predaceous on nematodes, since none of these five forms produce their spores in chains. However among the fungi found destructive to nematodes in agar-plate cultures planted with decaying vegetable materials catenulate sporulation very similar to that known in the Zoopagaceae occurs in representatives of the group of minute aerially sporiferous organisms that have been customarily referred to *Actinomyces,* though a genus of less ambiguous application is now available—if the lack of a Latin diagnosis can be overlooked—in *Streptomyces* Waksm. & Henr. (43). These organisms, which from their morphology seem best referable to the Phycomycetes, include not only many species parasitic on nematodes (*Bunonema* is attacked especially often) but also species destructive to various amoebae and to testaceous rhizopods of such genera as *Euglypha, Geococcus, Heleopera, Sphenoderia,* and *Trinema.*

Truly endogenous development of reproductive bodies in linear arrangement within basally attached unbranched filaments occurs certainly in a group of curious animal-inhabiting organisms, somewhat unfamiliar to mycologists though presumably referable to the Phycomycetes, of which the first representatives were made known by Leidy (24, 25, 26, 27) nearly a century ago in his original descriptions of *Enterobryus elegans, Enterobryus spiralis, Enterobryus attenuatus, Eccrina longa,* and *Eccrina moniliformis,*—all based on specimens found in the alimentary canals of different arthropods. *Enterobryus elegans* offers particular interest here as it was not only found attached to the mucous membrane of the small and the large intestine of its millipod host, *Julus marginatus* Say, but was also observed growing

from the exterior of the three nematode species—*Ascaris infecta* Leidy, *Streptosomum agile* Leidy, and *Thelastosomum attenuatum* Leidy—infesting the cavities of the viscera mentioned. Despite the development of *E. elegans* on nematodes, Leidy's account of this organism can hardly be considered directly suggestive of the Delaware fungus since in the relevant figures (27, pl. 1, fig. 1, e, f, i; pl. 4, fig. 28, b, c) its very few large propagative bodies, or "secondary cells" would seem to be formed through *Oidium*-like segmentation; and similar segmentation would likewise seem illustrated in the figures relating to "secondary-cell" production in *E. spiralis* (27, pl. 1, fig. 4, d) and *E. longa* (27, pl. 5, fig. 1–6). Closer resemblance to the Delaware fungus is, however, evident in the illustrations pertaining to asexual reproduction in some of the organisms more recently described, again from the digestive tubes of arthropods, as members of the group Eccrinides erected in 1905 by Léger and Duboscq (17) to include besides Leidy's two genera the type genus *Arundinella* (now *Arundinula*) then newly erected by them. This group, subsequently augmented through assimilation of *Amoebidium* Cienk. (4) and through addition (18, 19, 20, 21, 22, 23) of eight new genera, including three contributed by Poisson (32, 33, 34, 35, 36, 37), was in 1929 ranked by its authors (22) apparently as a subclass (Eccrinideae) in the Phycomycetes under which were subsumed two separate orders, the Eccrinales with three families and the Amoebidiales with one family. From the descriptions and figures given by Léger and Duboscq and by Poisson, the spores of the Eccrinales are formed endogenously. The "macroconidia" of these authors, though apparently corresponding to Leidy's "secondary cells," seem much less suggestive of oidia. Where the French investigators show relatively short thalli in process of forming the small reproductive bodies designated by them as "microspores," as, for example, in a specimen of *Parataeniella intermedia* delineated by Poisson (35, p. 205, fig. XX, E), it is easy to recognize general similarity to hyphal outgrowths of the Delaware fungus, such as those illustrated herein in figures 4, 10, 11, 12, and 13. Since my fungus has so far not been seen to produce any spores of strongly indurated character, grounds are lacking for any comparison with the seriately arranged, transversely oriented, thick-walled reproductive bodies of the Eccrinales, which the French writers term "spores durables," and which Poisson (36, p. 60, 65) took occasion to distinguish from the "cysts" of Thaxter's *Enterobryus compressus* (42) as well as from the "oospores" of Hauptfleisch's *Astreptonema longispora* (15), a related species first placed in the Saprolegniaceae but later (16) surrendered to the protozoologists. My fungus has shown nothing in its sporangial outgrowths analogous to the expanded terminal "gland" present in some members of the Eccrinales, which by breaking down permits apical liberation most usually of microspores; and the disintegration of its

sporangial membrane seems too rapid and disorderly to afford any very close parallelism with the manner of dehiscence by lateral apertures that occurs among the Eccrinales more especially in the liberation of macrospores and resting spores. Further, the well-developed endoparasitic thallodic cells of my fungus have no recognizable equivalent in the Eccrinides, as the tubular thalli of those organisms are only slightly inserted into the host tissues, more or less after the manner familiar in the genus *Harpochytrium* Lagerheim; while *Asellaria Caulleryi*, a somewhat related branching parasite described by Poisson (37) from the intestines of isopods has no attachment at all. Production of amoebospores in addition to immobile spores, such as occurs in *Amoebidium parasiticum* Cienk. (4), where according to Cienkowski's account the amoebospores after their encystment may form several curved immotile spores endogenously, is wholly alien to my fungus. This distinctive type of reproduction, which led Bütschli (3, p. 611–614) and Minchin (31, p. 313–314) to subsume *A. parasiticum* under the Protozoa, is present in the genus *Paramoebidium* Lég. & Dub. (23) to the exclusion of endospore formation; and though absent throughout the order Eccrinales is held to be of primary significance in considerations touching the fundamental character and taxonomic relationships of the entire group.

The Delaware parasite, as has been intimated, appears best interpretable as a primitive member of the Entomophthoraceae. To provide a suitable place for it, a new genus is proposed under a name compounded of two words meaning "fertile" and "hair," respectively.

Gonimochaete Drechsler, gen. nov. Parasitus intra animalia viventia crescens; cellulis nutritis juvenilibus ejus septo in duos loculos identidem se dividentibus, his loculis inter se disjungentibus, itaque stato assumenti postremo ex corporibus unicellularibus disjunctis incoloratis constante; post mortem animalis corporibus vulgo globosis vel ellipsoideis, quoque omne protoplasma tradente dum hypham fertilem extra integumentum saepe in aerem rarius in materiam subjacentem vel ambientem proferente; quaque fertili hypha sporas immotas incoloratas in unicam seriem penitus gignente denique eas expellente simul membrana ipsius in parte superiore evanescente, tamen parte inferiore ascendente sursum muro clausi saepe paulo longius persistente.

Parasite growing within minute animals, its assimilative cells early in development repeatedly becoming divided by a cross-wall, and the two segments in each instance separating from one another, so that eventually the vegetative state consists of disjointed colorless unicellular bodies; the bodies commonly globose or prolate ellipsoidal in shape, each of them yielding all its protoplasm in putting forth a filamentous hypha which after emerging from the host integument most often projects into the air, though at times creeping over or extending into the surrounding material; each hypha producing internally a row of colorless immotile spores, then expelling them while simultaneously the upper portion of hyphal membrane collapses and vanishes, though the lower portion often becomes closed by a distal wall and then persists some time longer in an ascending posture.

Gonimochaete horridula Drechsler, sp. nov. Corpora assumentia incolorata, multa (saepius 15–80) in vermiculo nematoideo oriunda, in maturitate globosa vel elongato-ellipsoidea, plerumque 6–33 μ longa, 5.5–10.5 μ crassa, primo protoplasmatis disperse granulosi repleta, deinde ex uno extremo hypham fertilem promittentia itaque omnino se exinanientia; hyphis fertilibus incoloratis, vulgo plerumque ascendentibus (itaque conjunctim horridulis), 10–100 μ longis, 2.8–5 μ crassis, 2–12 sporas immotas intus gignentibus, binas vel ternas vel quaternas leniter eas deinde expellentibus, postremo eas apice clausa partis inferioris vacuae 5–80 μ longae sustinentibus; sporis incoloratis, cylindraceis, utrimque inaequaliter rotundatis vel oblique rotundo-truncatis, 4–9.5 μ longis, 3–4.2 μ crassis, dejectis gemmam glutinosam 1.5–2.5 μ longam 1.5–2 μ crassam saepe oblique ex uno extremo emittentibus.

Habitat in *Acrobeloideo* sp. in foliis *Aceris rubri* putrescentibus prope Georgetown, Delaware.

Assimilative bodies colorless, often developing in numbers from 15 to 80 in an individual nematode host, when full grown mostly 6 to 33 μ long and 5.5 to 10.5 μ wide, at first filled with dispersedly granular protoplasm, each later becoming completely evacuated in giving rise from one end to a single hypha; the hyphae colorless, often mostly ascending (and thus collectively offering a bristling appearance), 10 to 100 μ long, 2.8 to 5 μ wide, individually producing 2 to 12 immotile spores internally, then expelling them weakly mostly 2 or 3 or 4 at a time, and afterwards often holding them aloft at the closed tip of an empty lower part 5 to 80 μ in length; spores colorless, cylindrical, mostly rather irregularly rounded or somewhat obliquely truncate at both ends, 4 to 9.5 μ long, 3 to 4.2 μ wide, each eventually when lying on the substratum budding forth a bulbous adhesive protuberance, 1.5 to 2.5 μ long and 1.5 to 2 μ wide, usually somewhat obliquely from one of its ends.

Destroying nematodes belonging to a species of *Acrobeloides* it occurs in decaying leaves of *Acer rubrum* near Georgetown, Delaware.

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CYTOGEOGRAPHY OF EMILIA CASS. IN THE AMERICAS

J. T. BALDWIN, JR.[1]

Emilia Cass. is a genus of Compositae with, perhaps, a score or more species native to the tropics of the Old World. Two species are widespread in the American tropics as introduced weeds: *E. sonchifolia* (L.) DC. and *E. coccinea* (Sims) Sweet. Cytogeographic occurrence of these two species in the Americas is considered here.

E. sonchifolia (fig. 1) is an annual that, under favorable conditions, may come from seed to maturity within thirty days. In the Amazon Valley this species was observed to flower and fruit during every month in the year. Always the flowers were purplish pink, though the literature indicates those of some plants to be reddish. The chromosome number is $2n = 10$, $n = 5$ (figs. 2–4). The chromosomes were studied in aceto-carmine smears of leaves and of pollen mother cells. The following collections—of which specimens have been deposited in the Instituto Agronômico do Norte, U. S. National Museum, and New York Botanical Garden—were examined cytologically:

Source	*Habitat*	*n*	*2n*	*Collector's Number*
Pará, Brazil				
Oriximiná	mandioca field		10	*Baldwin 2973*
Obidos	grassy area in town		10	" *2970*
Juruty Novo	sandy field		10	" *2995*
Fordlandia	golf course		10	" *2713*
Belterra	*Hevea* planting		10	" *2705*
Alemquer	field		10	" *2969*
Bragança	railroad bank		10	" *4024*
Belem	*Lonchocarpus* planting	5	10	" *2704*
Amazonas, Brazil				
Manáos	public square		10	" *2784*
Guajará-Mirim	railroad bank		10	" *3148*
Porto Velho	railroad bank		10	" .....
Rio de Janeiro, Brazil	weed in garden		10	" *4577*
Zandary Field, Surinam	edge of airfield		10	" *4579*
Waller Field, Trinidad	edge of airfield		10	" *4580*

[1] Observations on which this report are based were made while the writer was an agent for the U. S. Department of Agriculture and were incidental to assignment in South America. Appreciation is here expressed to Felisberto Camargo, Director of the Instituto Agronômico do Norte, Belem, Pará, for cordial coöperation, to Anna Ferraz for making the drawing of *E. sonchifolia*, to S. F. Blake for determining the identity of a specimen of *E. coccinea*, to the curators of the herbaria of the U. S. National Museum, Chicago Natural History Museum, New York Botanical Garden, and the University of Michigan for loans of specimens, and to the American Geographical Society for permission to reproduce the map.

The illustrations are published with the aid of the Marcus Lucien Underwood Memorial Fund.

FIG. 1. *Emilia sonchifolia* (L.) DC. in flower and fruit from Belem, Pará, Brazil. ×0.5. Drawn by Anna Ferraz.

The species usually occurs in dry, sandy situations, where it may form thick stands. It is not, however, a serious weed; it cannot compete with rank-growing vegetation.

E. coccinea is likewise annual. Its maturation is less rapid than that of *E. sonchifolia* and, in comparison with the latter species, is tetraploid:

FIGS. 2–5. Chromosomes of *Emilia*. FIGS. 2–4, *E. sonchifolia*, mitotic and meiotic (I & II) metaphases: $2n = 10$, $n = 5$. FIG. 5, *E. coccinea*, mitotic metaphase: $2n = 20$. $\times 2750$.

$2n = 20$ (fig. 5). It is sometimes planted for its attractive red flowers (Standley 1928), as in the Jardim Botanico do Rio de Janeiro (*Baldwin 4578*: $2n = 20$). Weeds from the following places were examined cytologically:

Source	*Habitat*	*2n*	*Collector's Number*
Pará, Brazil			
Fordlandia	golf course	20	*Baldwin 2712*
Belem	*Hevea* planting	20	" .....
Amazonas, Brazil			
Manáos	vacant lot	20	" *2792*
Labrea	beside path	20	" *2935*
Guajará-Mirim	railroad bank	20	" *3148A*
United States			
Fort Meyers, Lee Co., Florida		20	*P. C. Standley 73322*

Specimens are in the herbaria mentioned above.

E. coccinea, as a rule, prefers a more fertile and moister situation than *E. sonchifolia* does, and it has a more robust stature; it may be somewhat troublesome as a weed. The two species were found growing together at Fordlandia, Guajará-Mirim, Manáos, and Belem. Intermediacy between the species was not observed. Nor in herbarium material were intergradations noticed. The diploid-tetraploid relation may act as an hybridization barrier.

Observations on these two species are in agreement with the statement of Cockayne et al. (1932) relative to the flora of New Zealand: "the exotics for the most part are annuals, occasionally biennials, in form unlike nearly all the indigenous species, usually producing a much greater number of seeds, with more rapid germinating power and probably greater viability. As for their habitats, the exotics affect cultivated ground and such as has been laid bare in the process of settlement—they are, as it were, the companions of man."

Ochse (1931) and Merrill (1943) indicate that whole plants of *Emilia* serve in the East as either cooked or raw food: such use in the Americas is not known to the writer. Except for the degree to which *E. coccinea* has been planted as an ornamental, spread of the genus in this hemisphere seems to have been dependent wholly upon chance. Entry of both species was apparently from the Atlantic side (figs. 6, 7). In spite of the fact that suitable habitats in the Amazon Valley are at distant points in vast stretches of for-

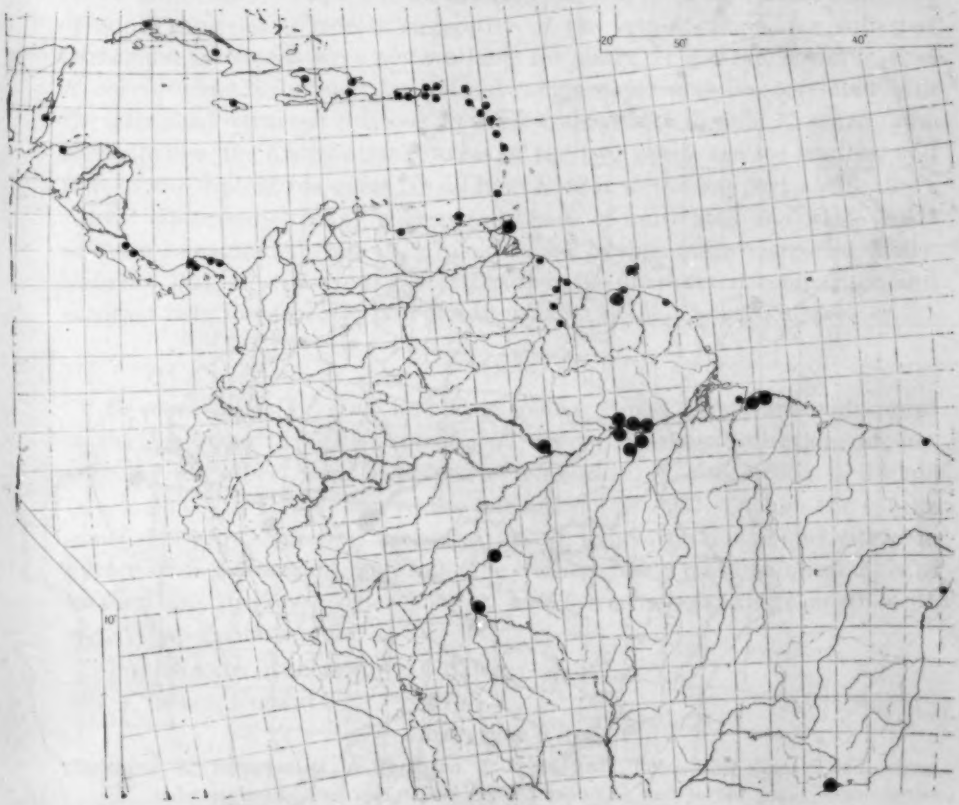

FIG. 6. Distribution of *E. sonchifolia* in the western hemisphere: big circles, specimens examined cytologically; little circles, specimens in herbaria.

est, occurrence there is rather marked. Movement into the interior has been along routes of travel and is in large measure reflection of the extent in time and space that man has disturbed the vegetation. Consequently, it is not surprising to find *E. sonchifolia* along both the railroads in the Amazon Valley—the Bragança and the Madeira-Mamoré, on both the Belterra and the Fordlandia rubber plantations, and along the Amazon. But it is worthy of record that at this date the species seems not to occur along the Rio Negro between

Manáos and the Venezuelan border, nor along the Solimoes, Purús, Juruá, and Marañon, nor in the rather thickly settled Acre Territory of Brazil and the adjacent low country of Bolivia, nor in Matto Grosso about the old towns of Corumbá, Cuyabá, and Rosario Oéste. In due time the plant will doubtless

FIG. 7. Distribution of *E. coccinea* in the western hemisphere: big circles, specimens examined cytologically; little circles, specimens in herbaria.

become established in those places: the situations seem favorable, and the species has effective means of transport; it was, for instance, one of eight Compositae that by natural means covered the twenty-five miles from Java to Krakatau, where it entered into the flora (Ridley 1930).

As revealed in this study, *E. sonchifolia* (fig. 6) has a range from ca. 23 degrees north to ca. 23 degrees south; *E. coccinea* (fig. 7), from ca. 29 degrees north to ca. 24 degrees south. Inclusion by Small (1933) of Florida within the range of *E. sonchifolia* is questioned. The species has undoubtedly been introduced there, but it seems not to have survived as an integral part of the flora, whereas *E. coccinea* is a not uncommon weed in southern Florida. It is considered that the northern occurrence of the two species is rather correctly shown on the maps, but the distribution mapped here for the continent of South America is merely suggestive of the actual ranges, for sufficient herbarium specimens were not available for study. It is clear, however, that *E. coccinea* has the greater latitudinal range, which may be correlated with the tetraploid nature of this species as contrasted with diploid *E. sonchifolia*. Nevertheless, the distributional areas of the two weeds are too similar, and that of the diploid too great, to adduce *Emilia* to the support of Huxley's (1943) statement: "Many widespread weeds of cultivated and waste lands are also tetraploid forms, the diploid types having quite restricted distribution." But, of course, one recognizes that for purposes of comparison and contrast only intraspecific polyploidy usually has much significance.

SUMMARY

E. sonchifolia (L.) DC. and *E. coccinea* (Sims) Sweet are widespread in the American tropics as introduced weeds. Fourteen collections of one, seven of the other, were examined cytologically. *E. sonchifolia* is diploid ($n = 5$, $2n = 10$), and *E. coccinea* is tetraploid ($2n = 20$). Though the species sometimes grow together, no indication of hybridity was found either in nature or in herbarium material. The diploid plant matures quicker, is of smaller size, prefers a drier habitat, and has a less extensive north-south range than the tetraploid.

THE BLANDY EXPERIMENTAL FARM
BOYCE, VIRGINIA

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BULLETIN OF THE TORREY BOTANICAL CLUB
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JEROME BOG, A PEAT-FILLED "CAROLINA BAY"

MURRAY F. BUELL

This study presents a description and the dynamic relationships of the bog vegetation characteristic of peat-filled "Carolina bays." The somewhat similar "pocosin" or "bayland" vegetation of the low, flat peatlands of eastern North Carolina has been described by Wells (1928, 1932), and by Dachnowski-Stokes and Wells (1929). More recently Wells (1942) has summarized our knowledge of the bog vegetation on the southern coastal plain. Yet no previous detailed study has been made of the vegetation of the peat-filled lake basins of this area. This paper is the result of such an investigation. It is concerned with a strictly delimited bog area giving a correlation of the distribution of the communities with certain physiographic features characteristic of the basin and its peat deposit. Besides the vegetation study, further information is added to our knowledge of the "Carolina bays" in the profiles showing the shape of the basin and the peat deposit which has accumulated in it.

This description of the basin may help a little in explaining the origin of a very perplexing physiographic feature. The elliptical depression occupied by this bog is one of a large number of similar basins in the region. Melton and Schriever (1933) gave the first detailed description of these remarkable depressions on the coastal plain and suggested a meteorite origin. Cooke (1934) and Johnson (1937) have both been critical of this hypothesis and have made other suggestions regarding the origin of the bays. Cooke believes they were formed by currents in coastal lagoons. Johnson proposed a theory of complex origin postulating a combination of artesian springs and underground solution causing subsidence together with lacustrine modification. All studies pertaining to the bays have been recently summarized by Johnson (1942).

Jerome bog is a perfect example of the "Carolina bays." It occurs in a sandy plain astride the Bladen–Cumberland County boundary line, just east of the hamlet of Jerome, North Carolina. It is almost perfectly elliptical with its long axis running northwest-southeast. There is a ridge of coarse white sand rising to about ten feet above the level of the bog at the southeast end, diminishing gradually northwestward around the margin of the bog and absent entirely at the northwestern end. Its height at the southwest end has been reduced by wind erosion at some earlier period, much of the sand having been blown toward the northeast. The vegetation of the sand ridge as well as the sand plain to the west and northwest is the longleaf

pine–turkey oak type (*Pinus palustris—Quercus catesbaei*) described by Wells and Shunk in 1931. There is some cultivated land west of the bog. To the northeast is a swamp into which the bog drains. Bog vegetation occupies a small bay just to the east and a low area toward the south.

The process by which such lake basins were filled in by peat must have been similar to those described for the few remaining bog lakes in this vicinity (Buell 1939).

METHODS

Peat profiles were obtained by sampling the deposit at 250-foot intervals along both the long diameter and the short diameter of the bog except across the northwest end where 500-foot intervals were used. Samples were taken with an American Peat Sampler (Davis type) at one-foot vertical intervals. The datum of reference for constructing the profiles was the bog surface, which was assumed to be level.

Levels were run to determine the corresponding height of the bog at the southeast end and at the drainage outlet. An arbitrary bench mark was selected half way along the east side of the bog and a traverse run to the southeast end and the outlet respectively. At the southeast end a line was run away from the bog up over the sand ridge while another was run out onto the bog itself. Although the unstable surface precluded accurate leveling, this line was continued 600 feet from the margin. Numerous readings were taken from three different places established along this line. These readings were of points on the bog surface taken at random. The bog level arrived at in each case is the average of the readings so obtained. Similar readings were taken on the bog surface 150 feet southeast of the outlet.

The survey of the vegetation was made along the same transects as the peat profiles. At each station where borings were taken the species present were listed and their abundance recorded using a scale of five. This listing and estimate of species abundance at each station together with general observations during the course of the field work are the basis of the description and discussion of the vegetation which follows.

THE BOG PROFILES

The basin in which the bog occurs has a broad, shallow shelf at the northwest end which drops more or less abruptly to the deepest point at the center lying in a trough-like depression extending to the southeast end. The profile of the long diameter reveals a broad shelf descending gradually from the northwest end for about 2250 feet at which point it is overlain by about four feet of peat (fig. 1). Here the shelf ends abruptly in a comparatively steep drop to the center which, a thousand feet farther on, is overlain by eleven feet of deposits. Southeastward the basin continues slightly shallower,

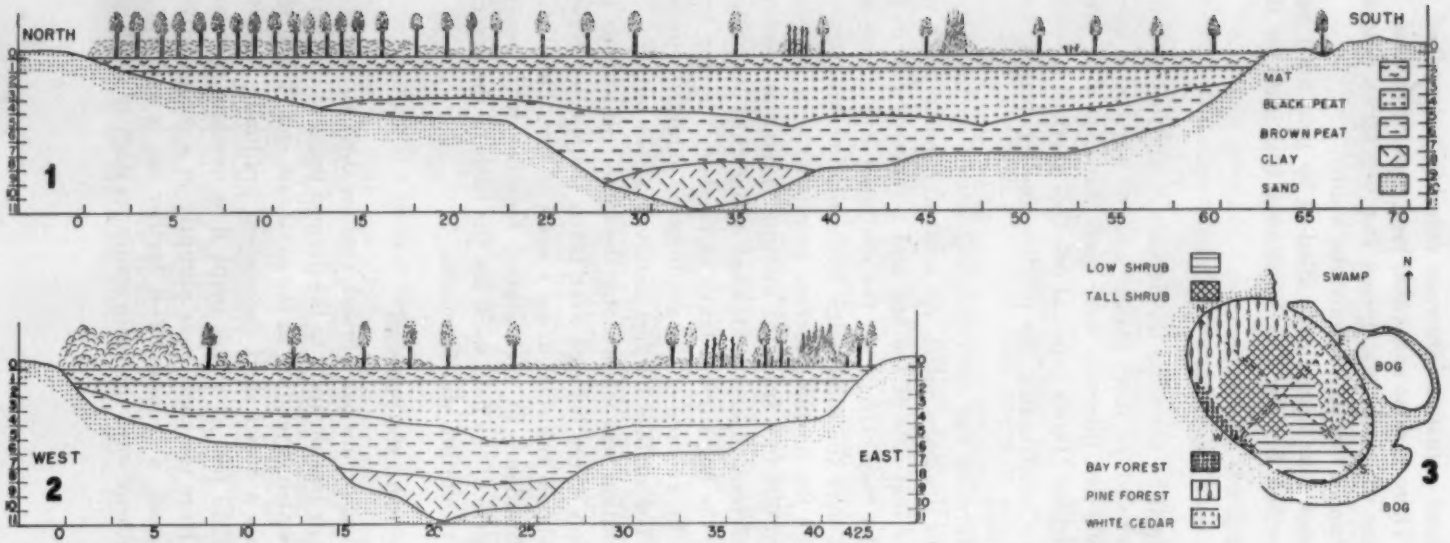

FIG. 1. Profile of Jerome bog along the long diameter. Diagram of vegetation shows the pine forest extending about 2,000 feet from the north end. The tall shrub community ends about 1,000 feet farther on. The low shrub community occupies the rest of the transect except where it cuts through a clump of dead white cedars at about 3,100 feet and the living white cedar forest at 4,600 feet. At 4,250 feet is a clump of *Cyrilla racemiflora*. At 6,250 feet is the sand bar, at 6,500 feet the bog lagoon. The profile of the sand rim is correct but the scale is about $\frac{1}{10}$th that used for the bog profile, its maximum height at 6,850 feet being about equal to the greatest depth of the basin. The vertical scale below the bog surface is given in feet, the horizontal scale is in hundreds of feet. FIG. 2. Profile along the short diameter. At the west end is the bay forest. Between the bay forest and a point about 2,000 feet from the west end is the tall shrub community. The low shrub community occupies the center but shows a gradual transition eastward to the tall shrub community. Burned and living groves of white cedar are shown toward the eastern margin. Scale is the same as in figure 1. FIG. 3. Map of Jerome bog showing distribution of plant communities and location of the transects. For scale compare figures 1, 2.

the bottom rising only gradually, until at about 5500 feet from the northwest end it rises abruptly from a depth of six feet to a low sand bar 750 feet beyond. Behind the sand bar is a bog "lagoon" and finally the rapid rise to the top of the sand rim which reaches a maximum height of ten feet above the bog at a point 450 feet beyond the margin. Hence the height of the sand rim above the bog surface is about equal to the greatest depth of the bog.

The profile along the short diameter, that from the east to the west sides of the bog, shows that the deeper part of the basin is a trough with a broad shelf on either side (fig. 2). On the east side of the trough the bottom rises in a series of two benches, a lower, broader one of six feet depth, an upper, narrower one of four feet depth. On the other hand, west of the trough the slope is continuous.

For the purpose of this present study the bog deposits are classified simply as clay, brown peat, and black peat overlying each other in that order. The clay is white and toward the bottom is mixed with varying amounts of the underlying coarse sand. Toward the top it contains bits of wood and other plant fragments. The brown peat differs considerably from place to place. It contains varying amounts of partially decomposed macroscopic fragments and here and there an abundance of logs that occasionally are so numerous as to make boring very difficult. Pollen has been well preserved and is abundant in this peat. On the other hand the black peat that overlies it is very fine, soft and sticky when wet, and dries to a hard, brittle mass. It consists of small bits of charred plant fragments and quantities of fine charcoal. Pollen is fairly abundant in the lower portion of the black peat but in the upper foot it is neither abundant nor well preserved. The surface of the bog is a continuous thick, coarse, tough mat of tree roots and the roots and rhizomes of shrubs.

The stratification of these types is not uniform. For instance the black peat is much deeper in the center and on the east side than on the west. The surface of the clay tends to dome up over the deepest point and the deposit is thicker over the west edge of the depression than the east.

The use of the bog surface as a datum of reference may be questioned. One gets the impression of a perfectly level surface in crossing the bog in any direction and all evidence accumulated suggests no reason to expect the contrary. Levels run six hundred feet out upon the open bog at the southeast end indicated a perfectly level surface. Although the outlet where the stream leaves the bay was found to be 3.6 feet below the level determined for the southeast end, the bog surface rises steeply from this outlet. At a point on the bog only 150 feet back of the outlet the average of 20 readings taken at random showed a rise of 1.5 feet in that short distance.

THE VEGETATION

The entire bog area is covered with a dense growth of shrubs throughout, in part as an understory in bog forests but dominating as such over the larger part of the bog. On much of the bog the shrubs are relatively low, from three to four feet, forming an open "pocosin" which includes roughly the central and southern portion of the bog and overlies the deepest part of the peat deposit. This will be designated the low shrub community in the following discussion. Contiguous with this on three sides, east, west, and north, is a dense growth of similar but taller shrub vegetation, the tall shrub community, averaging from twelve to fifteen feet. This community is exceedingly difficult to penetrate and one must cut his way through to make any headway at all. Throughout both of these areas in which the shrubs dominate there is a liberal scattering of widely spaced pocosin pines, *Pinus serotina* Michx. Toward the east and west sides and over the whole north end of the bog, trees dominate the vegetation. On the east is a strip of white cedar, *Chamaecyparis thyoides* (L.) B. S. P., on the west the bay forest community, and at the north end a forest of pocosin pine. In each of these the understory of shrubs is very dense but not quite so impenetrable as the tall shrub vegetation of the open part of the bog. Along the narrow bog margin where the peat and the sand meet there is another distinct community of trees and shrubs. *Sphagnum* is present throughout although nowhere in great abundance (see figure 3).

The communities are rather distinctive in their composition although certain species are conspicuous elements of some or all of them. For instance *Pinus serotina* and *Smilax laurifolia* L. are universally present, although the former assumes a position of dominance in the forest at the north end while the latter reaches its maximum development in the densest part of the tall shrub, where it very effectively ties the mass together with its large, long, thorny stems.

The low shrub and tall shrub are alike in composition, the latter being simply a later stage in the uninterrupted development of the former. The low shrub community is in general poorer in species. Certain herbaceous plants, specifically *Pteridium latiusculum* (Desv.) Hieron., *Sarracenia purpurea* L., and *Andropogon glomeratus* (Walt.) B. S. P. are entirely confined to this community. Elsewhere herbs are conspicuously absent except along the margin. Especially abundant and contributing as much as anything to the physiognomy of the community is *Zenobia cassinefolia* (Vent.) Pollard. *Chamaedaphne calyculata* (L.) Moench. and *Clethra alnifolia* L. are also both largely limited to the more open areas, the former becoming the dominant species locally. The presence of *Smilax laurifolia* is impressive, its scattered plants adding immensely to the tangle of the community. *Clethra* is the least abundant.

The taller shrub community represents less disturbed portions of the shrub bog and consequently a somewhat more mature stage in the development of the vegetation. Here there is a greater variety of species than in the low shrub community. The principal shrubs roughly in order of their contribution to the composition of the tall shrub community are as follows: *Ilex lucida* (Ait.) T. and G., *Smilax laurifolia* L., *Pieris nitida* B. and H. (locally dominating), *Zenobia cassinefolia, Ilex laevigata* (Pursh) Gray, *Kalmia angustifolia* L., *Lyonia ligustrina* var. *foliosiflora* (Michx.) Fern., *Itea virginica* L., and a scattering of *Amelanchier oblongifolia* (T. and G.) Roemer, *Aronia arbutifolia* (L.) Ell., and *Viburnum nudum* L. Small trees of *Acer rubrum* L., *Magnolia virginiana* L., and *Persea pubescens* (Pursh) Sarg. are very abundant.

The bay forest represented by a narrow strip along the west side is relatively poorer in species. Here *Acer rubrum* and *Magnolia virginiana* are dominant. *Vaccinium australe* Small is the principal understory shrub. Seedlings of *Acer rubrum* are abundant. The less common elements are *Persea pubescens, Ilex lucida, Itea virginica,* and *Smilax laurifolia.*

The white cedar forest is very poorly developed on this bog. It occurs as small, isolated stands along the east side and as small clumps out toward the center. Fire has recently destroyed some of them. The tall shrub bog grows intimately up against each stand and forms impenetrable thickets between them. The principal species associated with the white cedar is *Pieris nitida.* Such white cedar forests, their origin and successional status, have been described in an earlier paper (Buell & Cain 1943).

The pocosin pine forest at the north end occurs on a relatively thin layer of peat overlying the broad, gently sloping sandy shelf. The pines are large and closely enough spaced to produce a definite pine-dominated community. The understory is made up of large shrubs and small trees of the species which characterize the tall shrub community described above.

The bog margin community growing where the peat thins out to the coarse sandy soil of the surrounding upland includes a variety of shrubs not occurring, or if so very rarely, upon the bog proper. These are as follows: *Myrica cerifera* L., *Gordonia lasianthus* L., *Azalea atlantica* Ashe, *Vaccinium crassifolium* Andr., *Cyrilla racemiflora* L., *Ilex glabra* (L.) Gray, *Pieris mariana* (L.) B. and H., and *Nyssa biflora* Walt.

DISCUSSION

Jerome bog represents an ancient lake that has been filled in with a peat deposit. Its basin is one of a large number of such elliptical depressions (Melton and Schriever estimate about 1500 while Johnson believes there must be tens or even hundreds of thousands) on the coastal plain of the Carolinas. Many of the smaller ones may never have contained permanent

lakes. A very large proportion of them did and most of these are now filled with peat and support very much the same vegetation complex as Jerome bog. Several lakes in various stages of being filled in are still present in the vicinity. The process by which these lakes are being filled in has already been described (Buell 1939). The peat which is accumulating in these lakes today is a black, mucky deposit similar to that in the upper levels of Jerome bog. The color of this deposit is the result of the fires that occur frequently on the surrounding bog, the fine charcoal washing into the lake and settling along with the unburned plant fragments. The upper foot of the black peat may represent peat partially burned in situ, for peat fires often occur in the coastal plain bogs. However, since all but the top layer of black peat has a liberal mixture of pollen and unburned fragments it seems most probable that, with the possible exception of this top foot, it represents a subaqueous deposit. That this is so is further indicated by the greater depth of the black peat in the center and the east portion of the bog compared with the west side where the brown peat occurs within two feet or less of the surface. The "Carolina bay" lakes fill in most rapidly on the west side, slowest on the east, so that the bog lakes of today lie off center on the east side. With this in mind, the distribution of the black and the brown peat suggests that when fires first became common on the coastal plain, i.e., probably either with the advent of man upon the scene or at a time of a shift to a drier climate, Jerome bog was a lake with but a marginal bog. It might well have appeared as Little Singletary Lake immediately south of it appears today (see figure 4) or any other of the bog lakes in the vicinity. It is also clear that the coastal plain has never been completely free from fire during the entire history of the bog, since small amounts of charred fragments are found even to the bottom of the brown peat.

As far as the present vegetation is concerned there is no question that fire is and has been for a long time the dominant factor concerned in the control of the communities. Fire-scarred pine trunks and charred stumps of fallen trees are common. The universal distribution of the underlying black peat testifies to a long-continued addition of charcoal to the accumulating deposit. Yet certain physiographic features of the bog are correlated with the present distribution-pattern of the communities.

The shrub communities overlie, in general, the deepest parts of the peat deposit extending from the south end out toward the center and the east side (fig. 3). This represents the path of the most frequent and most severe fires. The prevailing wind is southwest. The probable source of most fires is in the vicinity of the nearest habitation just west of the south end of the bog. The low shrubs occupy the area most commonly swept by the fires. The tall shrubs represent merely an area that has received less recent ravages by fire and as such a later stage in the uninterrupted natural succession on the bog.

The location of the white cedar forest is to be explained by a fire of sufficient intensity to have created an open seed bed required by the cedar (Buell & Cain 1943). They do indeed occupy an area where occasional fires from the southwest end might be expected to reach their greatest intensity.

The bay forest along the west side demonstrates fairly well what the tall shrub would ultimately lead to were fires to be kept out. This forest is located on the west where by virtue of being on the side from which the prevailing winds come it is protected from the most intense fires. Any fires which pass

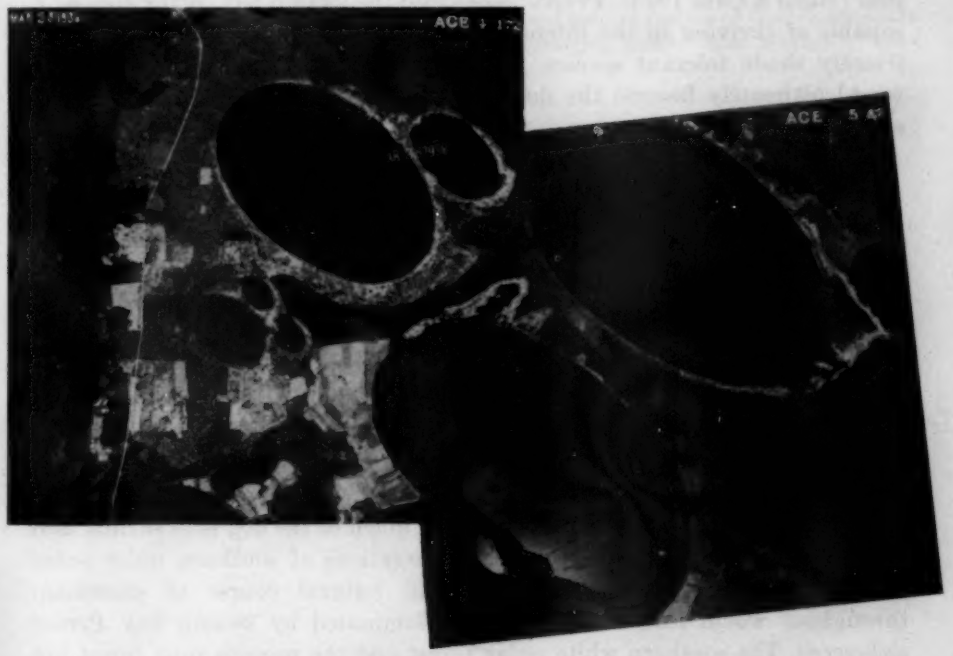

FIG. 4. Aerial photograph composite showing Jerome bog toward the northwest. Little Singletary Lake lies in the south central part of the area. Its bog margin is widest at the northwest end. Other "Carolina bays" both larger and smaller dot the area. (Photo by Agricultural Adjustment Administration.)

through it, fanned by the southwest wind, could not have first reached the full intensity attained after being driven through great masses of highly inflammable shrubbery. It is noticeable too that the black peat forms a thinner layer here than elsewhere along the east-west profile.

The pine forest at the northwest end occupies that portion of the bog underlain by the broad, gently sloping shelf upon which the peat deposit is thin. It is like the tall shrub community in composition with the exception of the abundance and size of the pines. The pines find conditions more favorable here than where the peat is deeper, a situation which may not be related

to the peat depth alone. They are larger and are numerous enough so that the aspect is that of a forest compared with the open shrub bog with its scattered trees. Were fires to be kept out, this, like the tall shrub community, would become a broadleaf bay forest, since small trees of sweet bay, swamp bay, and maple are present throughout.

The climax forest on the bog is a broadleaf bay forest. In the study of the successional role of southern white cedar in this part of the state it was found that the cedar does not replace itself in the natural course of succession (Buell & Cain 1943). *Persea pubescens*, the swamp bay, is the tree most capable of thriving in the intense shade of the cedar forest. That this extremely shade tolerant species, common throughout most of Jerome bog, would ultimately become the dominant tree of a climax bay forest seems extremely likely.

SUMMARY

1. Jerome bog occupies a "Carolina bay," one of a very large number of elliptical depressions on the coastal plain of the Carolinas. This basin is found to be deepest in the center with a trough continuing southward to an abrupt rise at the southeast end. At the northwest end is a broad, gently sloping shelf.

2. The deposit which has accumulated in this ancient lake basin consists of white clay in the deepest part, overlain by brown peat with scattered bits of charred fragments and, above this, black peat containing a high proportion of fine charcoal. The latter represents either the period since the advent of man bringing frequent fire or a drier climate, or both.

3. Fire holds the succession back so that much of the bog is in shrubs, and more severe burnings make occasional generations of southern white cedar possible locally. With fire protection the natural course of succession throughout would lead to a bay forest dominated by swamp bay *Persea pubescens*. The southern white cedar forest and the pocosin pine forest are merely subclimax types.

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THE EFFECT OF COLCHICINE AND ACENAPHTHENE IN COMBINATION WITH X-RAYS ON PLANT TISSUE—II[1]

MICHAEL LEVINE

MATERIALS AND METHODS

Root-tips on the bulbs of *Allium cepa* var. "Yellow Globe" were selected for this study. These were picked for their approximate uniformity of size and freedom from bruises and fungus infection. In one set of experiments, 18 bulbs of *Allium cepa* var. "Brigham Yellow Globe" sent to me by Dr. Henry A. Jones, U. S. Department of Agriculture, were used. These varied little in size, weight, and color. The bulbs used in the winter and early spring germinated promptly when set in water, but the dormancy of the summer crop was broken by exposure to low temperature (2°–5° C.) for 10–15 days. There were 15 sets of experiments, in each of which from 6 to 40 onions were used. Each set was started with a much larger number of bulbs than was actually used, for a small number were discarded during the first days of germination because of their failure to produce a satisfactory number of roots. After being weighed and recorded, the bulbs were placed on the mouths of cylindrical bottles of 240 ml. capacity filled with tap water. The water was changed daily and the bulbs washed in running water for a minute before they were returned to the jars.

In general, these plants were kept in water for 3–12 days before they were transferred to similar jars filled with an aqueous solution of 0.01 per cent colchicine in tap water. In preparation for irradiation after the colchicine exposure, the roots were washed in running water and placed on an inverted cardboard box, the bottom of which was perforated with 7 holes, each large enough to cradle a bulb. The bulbs were inverted so that the leaves or leaf ends were inserted into the holes and the root ends exposed to the air. The bulbs were then surrounded by walls of moist filter paper to prevent drying.

The x-ray machine employed delivered 95–133 roentgens per minute during the different exposures made. The voltage was 200 KV, 25 MA with a filter of 0.5 mm. copper and 3 mm. aluminum. The distance from the target varied for a given set of onions from 42 to 67 cm. Irradiations were made in single exposures with a total of 900r, 1500r, or 3000r. The actual exposure

[1] The first paper of this series appeared in Bull. Torrey Club 72: 563–574.

Publication of the illustrations was assisted by a contribution from the Montefiore Hospital.

time varied from 11¼ to 30 minutes. The time consumed by the irradiation varied from 17 minutes to 40 minutes. The non-x-rayed onions in a given experiment were removed from their cylinders for a period equal to that consumed for irradiation and precautions were taken with these also to prevent drying. The position of each bulb under the x-ray machine was then recorded, although the portal of the x-ray machine was open and no cone was used, so that the field was considered to be evenly covered by the x-rays. In several experiments, colchicine was replaced by acenaphthene. Cylinders similar to those used for colchicine were filled with a saturated solution of this substance. The wet roots were then gently powdered with acenaphthene crystals. Many of these adhered to the roots even after they were placed in water. Root-tips of treated and control onions were fixed at definite intervals in Bouin's, Carnoy's, and in Flemming's weak solution. The material was imbedded in paraffin and sections from 5 μ to 7½ μ in thickness were made. Flemming's triple stain and Heidenhain's iron-haematoxylin were used. Brilliant results were obtained with safranin counterstained with light green dissolved in oil of cloves.

COLCHICINIZED ROOT-TIPS OF THE ONION

Root-tips of *Allium cepa* exposed to colchicine have been studied by a number of investigators. Havas (1937a), Kostoff (1938a), Levan (1938), Mangenot (1938a,b), Shimamura (1939a), and others showed that colchicine causes hypertrophy of seedling parts as well as roots. While these swellings were referred to as "tumors," a modifying word like "colchicine" might be added to separate this type of growth from plant overgrowths such as crown-gall, potato wart, club-root, and possibly other plant hyperplasias.

A series of studies were made in this laboratory on concentrations, and it was found that the most appropriate was approximately 0.01 per cent, because it produced swellings after 24 hours that made it possible to gauge macroscopically the effects of irradiation.

The effect of the solution was then studied to determine the time required to produce root-tip hypertrophies, their behavior in prolonged exposures to colchicine, and their reaction on return to water. Three sets of preliminary experiments were made with 18 onions. These bulbs germinated in water at room temperature in 24 hours, and at 48 hours each bulb showed from 2 to 8 roots measuring from 1 to 2 cm.; at 5 days there were from 8 to 35, measuring from 1 to 4 cm. in length. On the eighth day the average number of roots per bulb was 30. Nine of these bulbs were placed in 0.01 per cent colchicine and the remainder left in water as controls. In 18–24 hours, small swellings began to appear just above the root-tips. At the end of 48 hours the tips were definitely swollen, measured 1–2 mm. in diameter, and were pointed at the extreme apex. Roots that had been formed just before immersion in the colchicine were transformed into swollen bulbous or club-like structures.

Continued exposure produced no decided increase in the size of these hypertrophies. The return of the bulbs to water after more than 200 hours in colchicine caused these roots to resume growth in 3–4 days; the growth started at the distal portion of the hypertrophy. Root-tips treated with colchicine were fixed after immersion for 6, 18, 24, 36, 48, 72, 96, 120, 144, and 200 hours, and at various times after their return to water.

These preliminary experiments were further made the basis for determining the time at which the metaphase stage in cell division appeared in greatest numbers, so as better to adjust the time when irradiation would be most effective. Although the hypertrophies were greatest at the 48th hour, cytological preparations showed that the greatest number of metaphases occurred earlier, confirming a report from this laboratory (Levine & Gelber 1943) that onion root-tips exposed to 0.01 per cent colchicine produced the maximum number of metaphases at about 24 hours.

Untreated onions were not uniform in leaf development and the colchicine solution alone seemed to have no effect on leaf growth.

Microscopic studies proved that the concentration of colchicine used was in itself not destructive to the cells, and roots exposed for as long as 200 hours exhibited only a reduction in the size of the meristematic zone. The extreme tip atrophied and many of the cells contained deeply stained homogeneous nuclei. Median longitudinal sections of such roots showed that the cells were hypertrophied but the zone of elongation remained inactive. There were areas of cellular activity that apparently represented secondary root meristems. The cells in these roots had few, if any, mitotic figures. The central or plerome cylinder of cells contained well differentiated nuclei and large vacuoles, while those in the periblem or mid-region and dermatogen or outer zone of cells contained large irregular nuclei, some of which were densely stained and undifferentiated. Small areas of destruction appeared to be due to the colchicine. In these cells, the walls were densely stained with the safranin, the cytoplasm was plasmolyzed, and in some there appeared to be fragments of densely stained granules possibly of nuclear origin. Cells in the branch root initials appeared quite normal, with a number of nuclei in mitosis, although the exact stages were not to be definitely established. The cells were embryonic in nature, with large, densely stained nuclei. When returned to water, the root-tips resumed growth and the bulbs produced a number of new roots.

The root-tips of the control onions grown in water for the same periods appeared normal. A small number of cells were found in all stages of nuclear and cell division.

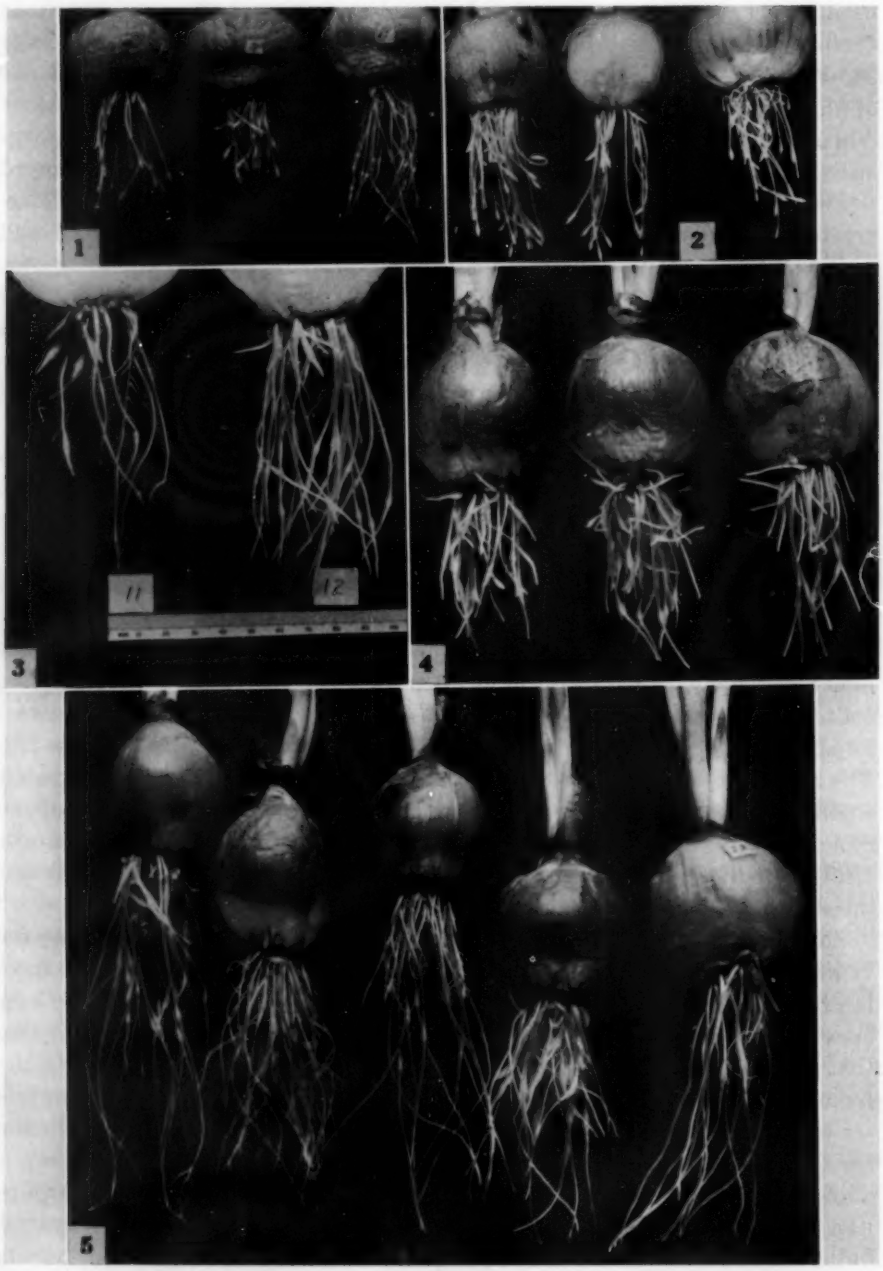
THE GROSS EFFECT OF COLCHICINE AND 900 ROENTGENS

In a series of 6 preliminary experiments, the effect of a single dose of x-rays of 900r on colchicinized root-tips of bulbs of the "Yellow Globe" var.

of *Allium cepa* were studied. One hundred and thirty bulbs were grown in fresh tap water from 3 to 12 days. Eighty-two were then colchicinized for 24, 48, 72, 120, 135, and 140 hours. Thirty-two others were irradiated and of that number 20 were colchicinized. There were 3 or 4 irradiated colchicinized bulbs in each of the 6 experiments. The controls, 98 in number, consisted of non-x-rayed colchicinized bulbs and others that were neither x-rayed nor colchicinized. In these experiments, the gross effect of the colchicine-treated root-tips were contrasted with those that were colchicinized and x-rayed. The ability of the colchicinized, hypertrophied root-tip to resume growth when returned to water gave a ready ocular demonstration of the effectiveness of the colchicine-x-ray treatment. When the colchicinized bulbs were returned to water, the distal portion of the bulbous tip resumed growth, leaving the swelling behind it. The irradiated colchicinized root-tips behaved differently as described in detail in the report that follows.

Of the bulbs selected for colchicine and irradiation studies 12 were immersed in colchicine for 120 hours after a five-day period of germination. Five bulbs were irradiated with 900r and immediately thereafter all were returned to water. The gross differences were studied between the colchicinized-x-rayed root-tips and those that were treated only with colchicine. All the roots of the colchicine-x-ray group appeared alive but for the presence of an occasional flaccid, water-soaked one, yet no outgrowth had taken place at the root-tips (fig. 1). Eight days after their return to water the colchicine controls produced extensive outgrowths from the bulbous tips showing no impairment of the meristem at the tip of the hypertrophy (fig. 1, bulb 12). The short swollen roots clustered around the bulb appear to have elongated slightly (bulbs 3, 7) but no definite outgrowth followed. The short bulbous root-tips on the colchicine controls (bulb 12) also failed to resume growth after the bulbs were replaced in water. This difference in behavior between the short and long roots has not been explained.

After germination for five days, 15 bulbs were exposed to colchicine for 72 hours, then irradiated with 900r and finally returned to water. Five days later, these bulbs had a small number of flaccid roots among the healthy long ones (fig. 2) which showed no evidence of having resumed growth. The bulbs that were not irradiated (fig. 3) underwent characteristic recovery with the formation of secondary roots. The roots of another group of 24 onions in this series of experiments were exposed to a similar concentration of colchicine for 48 hours. They were similarly irradiated and returned to water. Eleven and one-half days after the treatment there was an unquestionable resumption of growth of the swollen root-tips (fig. 4). These colchicine-x-rayed bulbs showed root extension of approximately 0.5 cm. Daily measurements of the length of the roots, however, showed the growth to be slow and suggested an elongation process rather than one due to cellular proliferation.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Growth ceased after the sixth or seventh day. Comparison with the controls indicated clearly that growth had occurred in the roots which were treated only with colchicine (fig. 5). The outgrowth in the control was more slender than the portion of the root above the hypertrophy. Roots without hypertrophies, apparently new roots, had developed from the bulbs on their return to water. Secondary roots were formed, many of which arose from the hypertrophied portion of the root.

The significance of these results made it necessary to further test the effects of the irradiation on the 48-hour-colchicinized root-tips. In this test 30 bulbs were used, and after a germination period of six days the bulbs were colchicinized for 48 hours, irradiated with 900r, and then returned to water. These were studied daily. The results confirmed the findings observed above. Bulbs colchicinized only and returned to water underwent the usual recovery with active growth from the hypertrophied root-tips. Long tenuous secondary roots were frequently developed. The control non-colchicinized bulbs that were kept in water for nine days and were x-rayed simultaneously with the colchicinized bulbs showed little effect after their return to water. The roots appeared to be active, the tips were normal and not twisted, a phenomenon observed after exposure to larger doses of x-rays. There was, however, a temporary arrest of growth.

Root-tips that were colchicinized for 24 hours and irradiated with 900r grew after they were returned to water. Those that were colchicinized for 135–140 hours and irradiated reacted like those that were irradiated after 120 hours exposure to colchicine.

These experiments show that exposure to 900r has a temporary retarding effect on growth of root-tips of the onion, but that when it is preceded by exposures to colchicine for more than 48 hours, complete inhibition of growth is attained without causing immediate death. Root-tips exposed to colchicine for 48 hours followed by 900r, become impaired in growth with complete exhaustion of growth 5–7 days after their return to normal conditions.

CYTOLOGICAL CHANGES INDUCED BY COLCHICINE AND 900R

Colchicine for 24 hours and 900r. Colchicinized and x-rayed roots were selected at random for microscopic examination from all the bulbs that were

Explanation of figures 1–5

FIG. 1. Bulbs exposed to colchicine for 120 hours; irradiation 900r; returned to water after treatment for 8 days. Bulb 12 not irradiated. ×0.6. FIG. 2. Bulbs exposed to colchicine 72 hours; irradiation 900r; 5 days after their return to water. ×0.75. FIG. 3. Bulbs from same series not irradiated, colchicinized for 3 days; 5 days after their return to water. ×0.25. FIG. 4. Bulbs exposed to colchicine for 48 hours; irradiation 900r; 11½ days in water after treatments. ×1. FIG. 5. Bulbs colchicinized for 2 days and then returned to water for 11½ days; not x-rayed. ×7.

The photomicrographs were made on W. W. Panchromatic M. plates in a Zeiss 35 cm. camera. The objectives used were Zeiss 2a, 10, 20, 90; eye piece Homol 1; bellows extension 50 to 100 cm.; filters K_2 and B.

subjected to these agents. Sections through the periblem were studied principally because these better exposed the largest number of dividing cells.

The untreated control root-tips kept in water for 15 days showed normal cellular structures with a moderate number of nuclear and cell divisions. Sections of root-tips made from the bulbs colchicinized for 24 hours and exposed to air for a period of 30–40 minutes (fig. 7), during which time other bulbs were x-rayed, presented no marked or recognizable influence of this treatment except for the colchicine-induced metaphases. In the calyptrogen or root cap of these root-tips, the nuclei were compact bodies, homogeneously stained with Flemming's triple stain. The dermatogen cells contained metaphase stages and occasional late telophases were observed with good spindles. There was evidence of fusion of chromosome masses, while the nuclei in the resting cells were well differentiated and the chromatin was stained brilliantly with gentian violet. The chromatin granules were distinct and appeared to be sharply defined as if some contraction or accumulation of the material had occurred. The cytoplasm in these cells was stained a faint orange. In these preparations there was evidence of a concentration of the granular elements in the cytoplasm, forming a close reticulum. There was no evidence of nuclear or cytoplasmic injury.

Under higher magnification (fig. 8), the chromosomes showed longitudinal splitting with few instances of chromosome clumping. The 24-hour-colchicine-treated root-tips irradiated with 900r were fixed two hours after their return to water. In these sections there was evidence of marked clumping of the chromosomes in the metaphase stage, although chromosomes occasionally separated from the fused masses could be recognized as being longitudinally split (fig. 9). A number of prophases appeared in these preparations which were apparently normal. A detailed study of the colchicinized and x-rayed root-tip cells is shown in fig. 10. Ring-shaped chromosomes such as reported by Marquardt (1938) and Sax (1941) were not infrequent.

The x-ray control plants not treated with colchicine but irradiated with 900r (fig. 11) were grown in water for 13 days 3 hours, irradiated and returned to water for 2 hours and 40 minutes before fixation. These tips showed few metaphases and less marked chromosomal aberrations than those treated with colchicine and x-rays. The clumping of the chromosomes was not strongly developed and split chromosomes were not infrequently found.

Root-tips that were colchicinized for 24 hours and irradiated with 900r grew after they were returned to water. Microscopically, these tips fixed eight days after their return to water showed that the cells were active and viable (fig. 12). The subsequent history of these roots was not followed in detail. Sections of the untreated control roots were normal; mitoses were frequent without any apparent abnormalities, in spite of their exposure to water for 21 days.

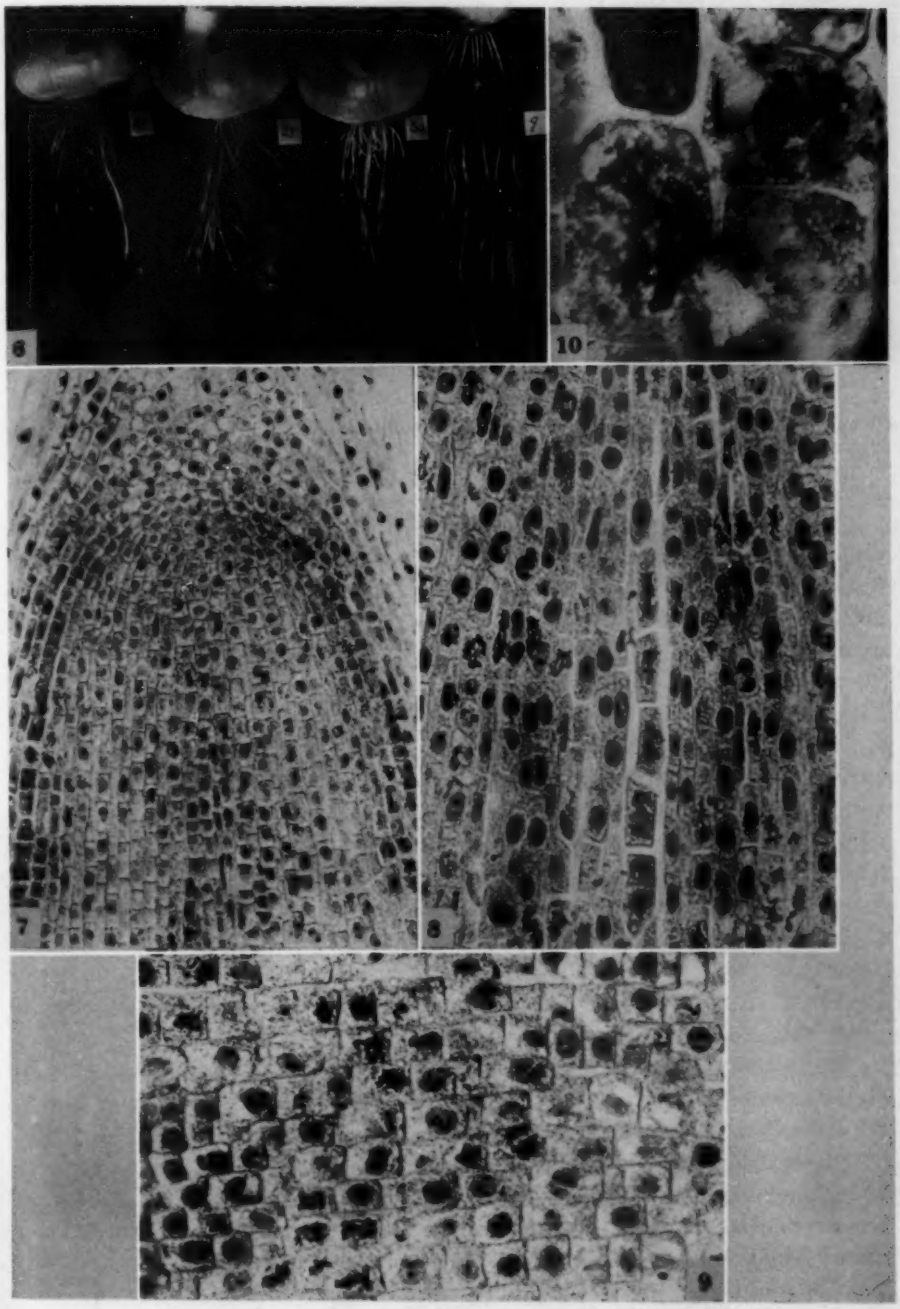


FIG. 6. Bulbs 21, 29, 30 exposed to a saturated solution of acenaphthene for 48 hours; irradiation 900r; returned to water 5 days. Bulb 9, no irradiation. × 0.6. FIG. 7. Exposed to colchicine 24 hours; to air 30–40 minutes. × 250. FIG. 8. Section of root-tip after 24 hours in colchicine. × 500. FIG. 9. Root-tip exposed to colchicine for 24 hours; irradiation 900r; fixed 2 hours after their return to water. × 500. FIG. 10. Selected cells from root-tip shown in figure 9. × 1800.

Colchicine for 48 hours and 900r. Root-tips exposed to colchicine for 48 hours, followed by irradiation with 900r, were fixed for microscopical examination at various intervals after their return to water. These were compared with the root-tips that were x-rayed or colchicinized only and returned to water for various periods of time. Serial sections of root-tips were made. These tips were fixed immediately after their removal from 44–51 hours exposure to colchicine before irradiation. In the root-tips colchicinized for 48 hours the cells of the elongation zone had become wider and only slightly longer and so had produced the characteristic bulge or swelling of the root-tip. The number of metaphases was fewer than after the 24-hour treatment and the chromosomes appeared to be fused and contracted, while fragmentation occurred. These observations were in accord with those of Levan (1938), Shimamura (1939a) and others. There appeared to be a number of masses of gentian-violet-staining material in some cells, most frequently but two. Their subsequent behavior could be interpreted as giving rise to polyploid lobulate nuclei.

The chromosomes in these preparations frequently appeared indistinguishable from those subjected to irradiation and suggested the effect described by Dustin and his students. The resting nuclei were densely stained. The cells were vacuolate and there appeared to be a more intensely staining granular structure in the cytoplasm. The peripheral cells, however, were vacuolized and the cytoplasm had a tendency to be stained more densely. The return of these colchicinized bulbs to water caused the root-tip to recover, as shown by its renewed ability to grow. The meristematic tissue, however, appeared to be less voluminous and the outgrowth from the bulbous tip resulted in a somewhat attenuated structure. Under certain conditions the entire bulbous root-tip became elongated before the root-tip resumed growth. Sections of root-tips from the same bulb made 24 hours after their return to water showed recovery from the metaphase stasis. Normal telophases occurred although there was some evidence of contracted, deeply stained nuclei and possibly dead cells. Sections of roots from the same bulbs in water 72 hours after their removal from colchicine showed various figures in mitotic stages of development and seemed apparently normal.

Bulbs treated in colchicine for 44–48 hours and irradiated with 900r were studied shortly after the x-ray exposure. The root-tips fixed one hour and 35 minutes after their return to water at the end of irradiation contained elongated chromosome masses (fig. 13), and highly vacuolized cells, some of which enclosed lobulate nuclei. The cytoplasm in these preparations appeared to be reticulate with densely staining granules lying in the meshwork. These observations were made repeatedly in several groups of bulbs studied. Sections of root-tips from the same bulbs 48 hours after the colchicine and x-ray treatment (fig. 14) showed slightly elongated, hypertrophied cells, although

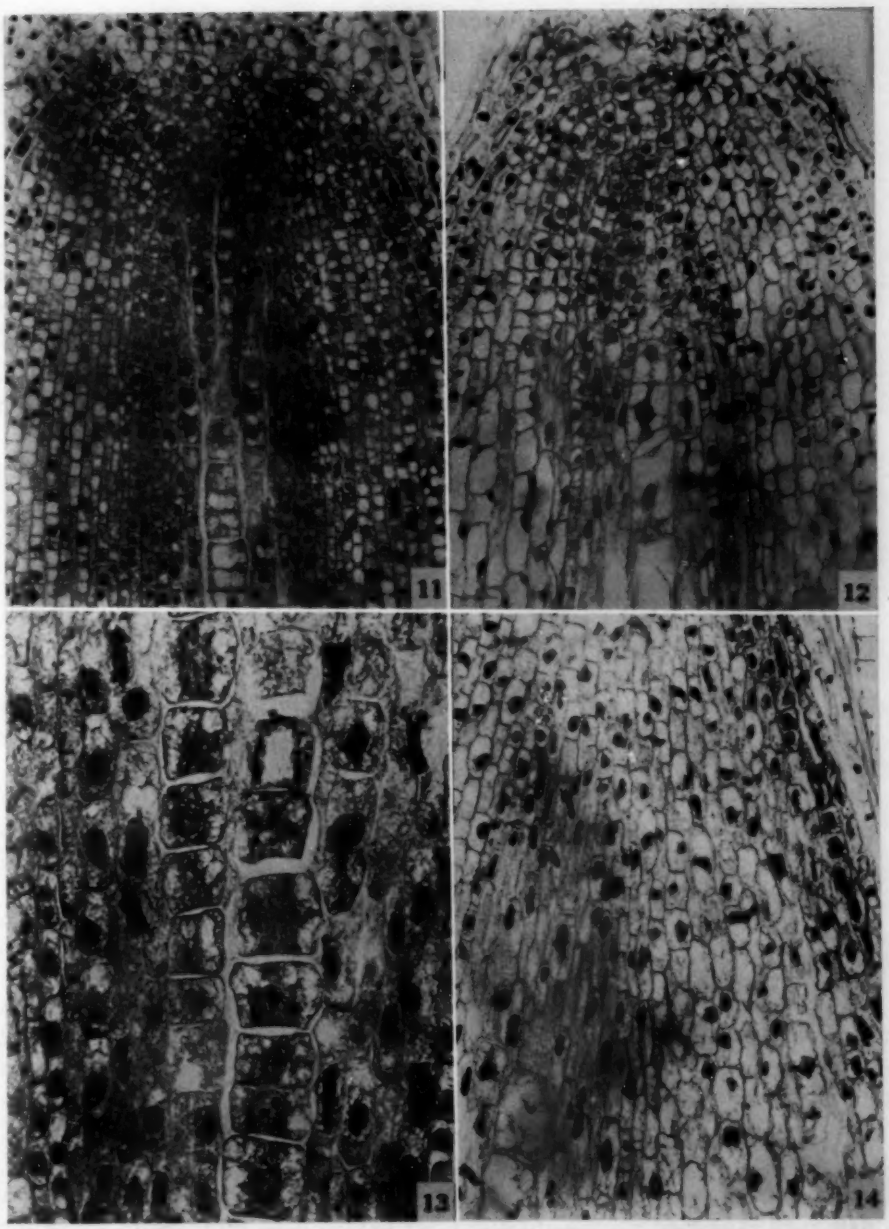


FIG. 11. Root-tip irradiated with 900r, fixed 2 hours and 40 minutes after its return to water. ×250. FIG. 12. Root-tip treated the same as that shown in figure 9; fixed 8 days after return to water. ×250. FIG. 13. Portion of root-tip exposed to colchicine 48 hours; irradiation 900r; fixed from water 1½ hours after irradiation. ×500. FIG. 14. Section of root-tip treated as in figure 13; fixed from water 48 hours after treatment. ×250.

they appeared to be arranged in regular tiers. The nuclei were irregular in shape; some were homogeneously stained and indicated injury. Many ruby-red-stained bodies appeared, apparently nucleoli; usually two were found in each cell. In the later stages, in which the roots were returned to water for 80 hours, there appeared to be recovery. Nuclear divisions were in progress and the intense cytoplasmic vacuolization had now disappeared (fig. 15). There was evidence in these preparations that the chromosome number had increased, but no chromosome counts were made. The outgrowths from these colchicinized-irradiated root-tips after their return to water had reduced but normal meristems; division stages were not abundant. The active cells were stained like normal meristematic tissue. The formation of secondary root meristems was unaffected by the colchicine-x-ray treatment. It seemed that these structures were formed after the effects of these stimuli were no longer present; few secondary roots were observed to develop.

Colchicine for 72 hours and 900r. Root-tips exposed to colchicine for 72 hours produced new outgrowths from the bulbous tips which grew uninterruptedly (fig. 3). Microscopic studies of the tips (fig. 16) made 4 days after their return to water showed a meristematic region of normal cells with a small number of nuclei in division. The periblem cells were vacuolate and some occasionally contained giant nuclei. These aberrant cells were in the hypertrophied portion of the root.

The colchicine-irradiated root-tips made no outgrowth from the bulbous tip 96 hours after their return to water (fig. 2). The cells in these root-tips were large and vacuolate (fig. 17) with large homogeneously stained nuclei. The plerome cells were slightly elongated, and the nuclei though somewhat large contained no distinct chromatic granules. The nucleoli were well differentiated and took the safranin brilliantly. The periblem cells showed evidence of injury and maturity. The vacuoles were large and the nuclei slightly lobulated. Growth in these cells was not followed beyond the fifth day after their return to water.

Colchicine for 125 hours and 900r. An examination of the outgrowths removed from the bulbous tip (fig. 3) which were produced by an exposure to the colchicine for 125 hours and then returned to water for 90 hours showed cytological structures similar to those of normal root-tips with approximately a normal distribution of mitotic figures (fig. 18). The area of the meristematic region appeared small.

The root-tips exposed to colchicine for 125 hours and irradiated with 900r were examined microscopically after having been returned to water for 90 hours. The cells were hypertrophied (figs. 1, 19); only the terminal portion, where the meristem would normally be, showed a small collection of cells with densely stained nuclei; no calyptrogen was present. The periblem

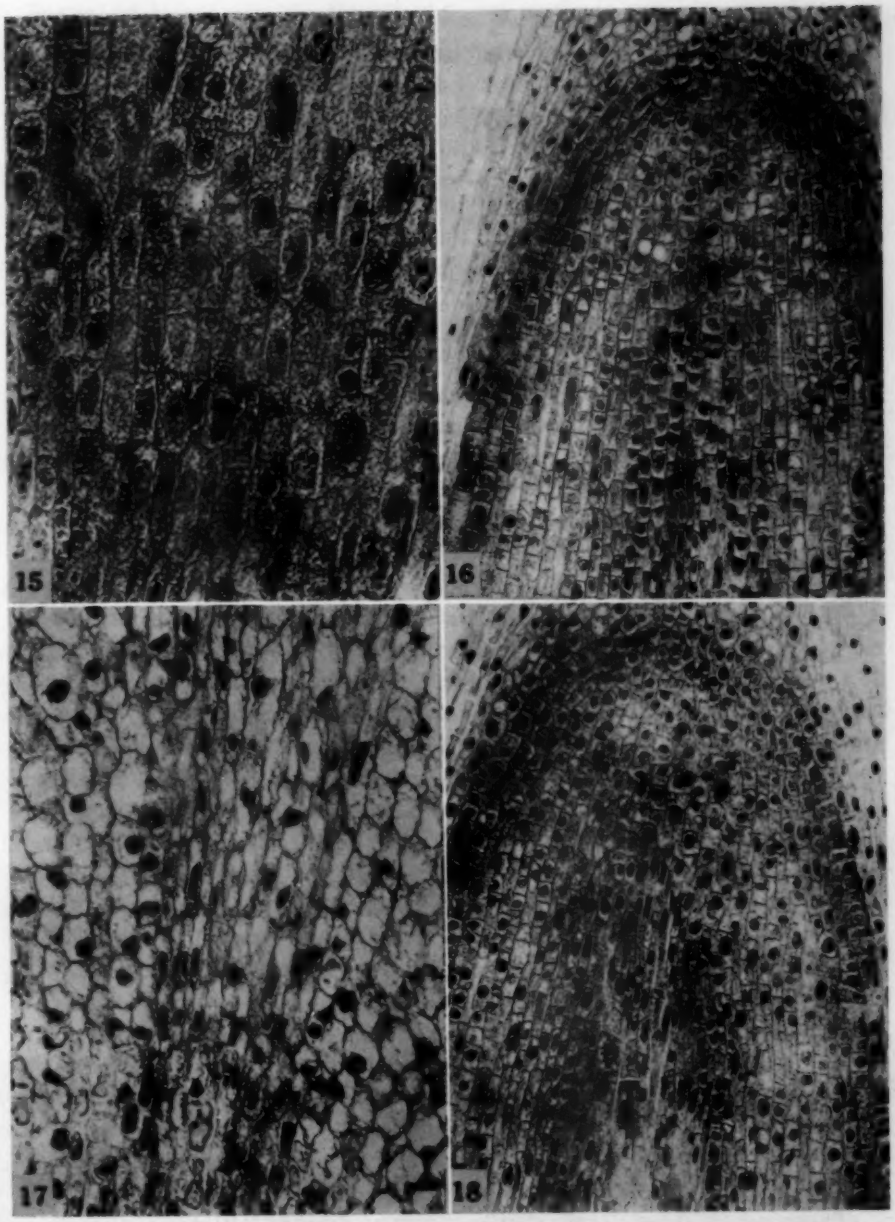


FIG. 15. Part of root-tip treated as in figure 13, fixed after being in water for 80 hours. ×500. FIG. 16. Section of root-tip after return to water for 96 hours; exposed to colchicine for 72 hours. ×250. FIG. 17. Section of root-tip after return to water for 96 hours; exposed to colchicine for 72 hours followed by 900r. ×250. FIG. 18. Root-tip exposed to colchicine for 125 hours, fixed 90 hours after return to water. ×250.

cells were large in size with irregularly shaped nuclei which were well differentiated. Evidence of nuclear lobulation occurred. The cytoplasm was strikingly fibrillar in nature and formed a reticulum which was well preserved by the fixative. The cells were not dead but evidently showed the influence of marked earlier disturbances. There were no outgrowths from these swellings eight days after their return to water.

Colchicine for 140 hours and 900r. Root-tips immersed in colchicine for 140 hours and followed by irradiation (900r) were fixed approximately one and one-half hours after their return to water. The meristematic area in these roots was reduced to empty cells, although a thin layer of deeply staining tissue below a degenerated root-cap was always present. There were some active cells surrounding the plerome, although division stages were not seen. The viability of these roots was represented principally by some few cells. Those in the plerome area were large with extensive vacuoles, and the nuclei seemed polyploid, for many were lobulate; while other cells were binucleate. The densely stained portions of the root appeared to be made of necrotized cells. Many cells in the periblem contained large vacuoles, while many were empty.

The root-tips colchicinized for 140 hours and irradiated with 900r, when examined microscopically after having been kept in water for 48 hours (fig. 20), contained active viable cells about the lower portion of the plerome. A densely stained necrotic tissue surrounded this cluster of cells in which the nuclei were lobed though densely stained. Large nuclei in hypertrophied cells were also present. Many of the cells had normal cytoplasm; some had a delicately reticulated cytoplasm while others were large and empty. The periblem cells now contained only a few nuclei; most of them were necrotized, with fragments of deeply stained bodies. Root-tips from this series, kept 8 days in water after irradiation, were flaccid. The upper portions of these roots were alive, however, for secondary root initials were present although none seemed to emerge. Irregular spiral thickenings of the vessels were noted in the central cylinder, while the cells of the secondary root meristems were in various stages of nuclear division. The irradiation effects were entirely absent at this period. Root-tips taken from bulbs exposed to colchicine for 140 hours, but with the irradiation treatment omitted, gave evidence of normal recovery of growth as described above. The upper part of these roots developed normal secondary branches. The roots at this stage of the experiment were in water before and after colchicine, a total of 24 days.

These results show clearly that root-tips exposed to 0.01 per cent aqueous solution of colchicine for 140–200 hours suffer no permanent effect on growth. When returned to water they recover, and new primary and secondary roots are formed.

The colchicinized root-tips irradiated with 900r show that the length of colchicine exposure influences recovery; long exposures (72–140 hours) followed by irradiation completely inhibit growth. The colchicinized controls make new growth after their return to water. With shorter colchicine exposures (48 hours and less) growth is still inhibited, yet the bulbous tips produce outgrowths from their distal portions. Obviously the inhibiting factor is not a function of the irradiation (900r), which had only a temporary retarding effect, but of the combined result of both agents. These gross observations are well supported by microscopic evidence. The short colchicine exposures followed by irradiation left unimpaired meristematic cells, which were capable of producing new growth. The long colchicine exposures coupled with 900r inhibited and impaired the fundamental tissues and no outgrowth occurred from the hypertrophies. Irradiated (900r) non-colchicinized root-tips failed to show the gross and microscopic changes induced by the application of both agents.

THE GROSS EFFECT OF COLCHICINE WITH 1500R OR 3000R

These investigations were made on a strain of selected onions of the "Brigham Yellow Globe" variety of *Allium cepa* together with bulbs of the "Yellow Globe" variety culled from the open market. These onions were germinated for 7–8 days after they had been chilled for 12–14 days to break their dormancy. The roots of these bulbs were then immersed in an aqueous solution of 0.01 per cent colchicine for various periods. Of the colchicinized onions some were x-rayed and returned to water. A number of bulbs were x-rayed only and an equal number were treated with neither colchicine nor x-rays.

In one experiment 18 bulbs of the "Brigham Yellow Globe" variety were used. These bulbs weighed from 58 to 94 g. and germinated uniformly eight days after they were placed in water; the number of roots which each produced varied. Leaves developed on all bulbs with only slight differences in number and in size. These bulbs were divided into two groups and six bulbs of each were set in the colchicine solution while three remained in water. After an exposure to colchicine for 48 hours five bulbs were irradiated with 1500r; two bulbs were not colchicinized but were irradiated only. In the other group, five bulbs were colchicinized and exposed to 3000r and two non-colchicinized bulbs were included in this exposure. One colchicinized and two untreated bulbs served as controls in each set.

The roots of these bulbs were studied at various intervals after treatment. The colchicinized bulbs (fig. 21, bulbs 2 and 7) that were given 1500r and 3000r respectively showed clearly 9 days after their return to water that growth of the meristem had been inhibited. The non-colchicinized bulbs irradiated with 3000r (bulb 13) showed considerable root injury. The roots

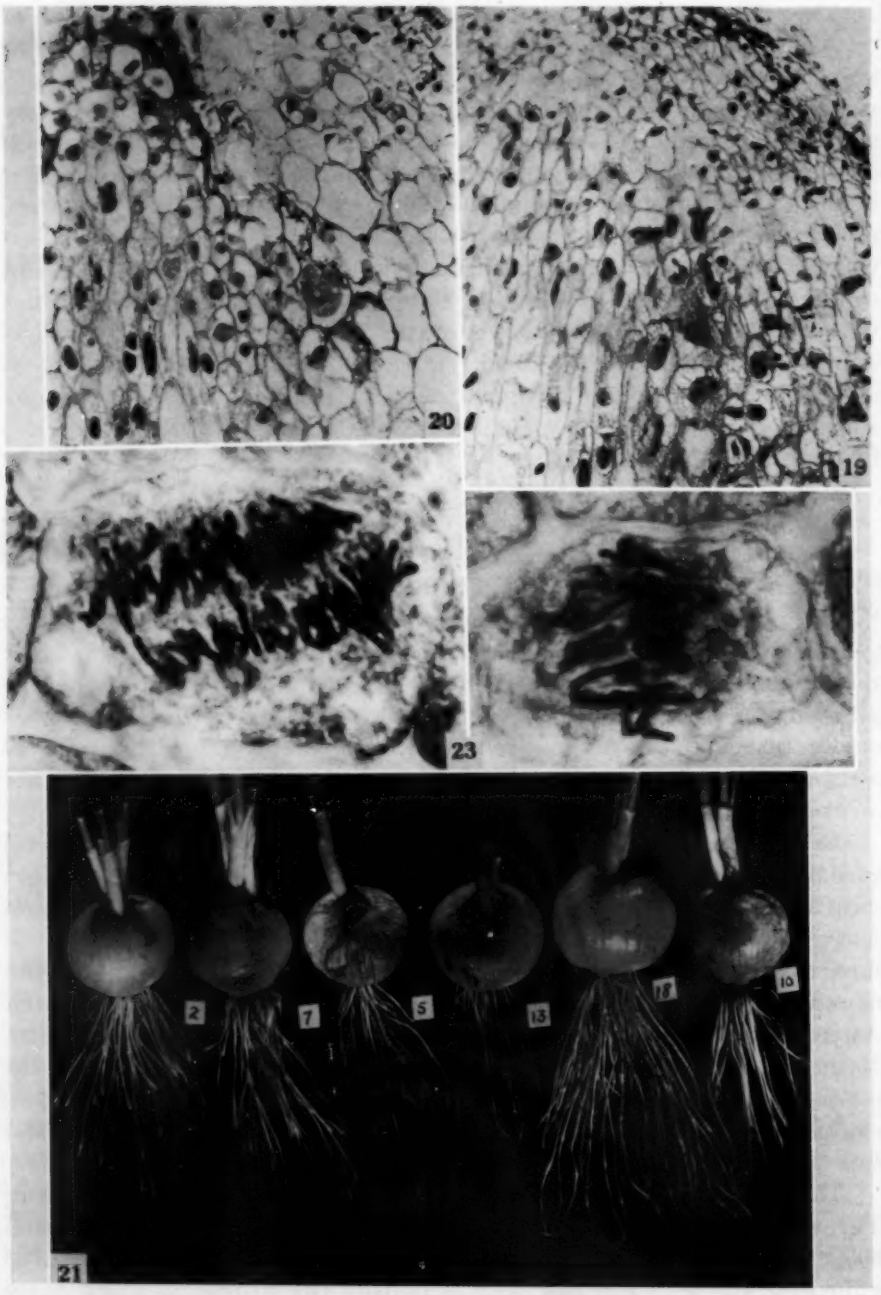


FIG. 19. Root-tip in colchicine for 125 hours; irradiation 900r; fixed after 90 hours in water. ×250. FIG. 20. Root-tip treated in colchicine 140 hours; irradiated with 900r; fixed after 48 hours in water. ×250. FIG. 21. Effect of colchicine and irradiation on root-tips. Bulb 7, colchicine and 3000r; 13, 3000r only; 2, colchicine and 1500r; 5, 1500r only; 18, colchicine only; in water 12 days after colchicine and x-rays; bulb 10, water only. ×0.6. FIG. 23. Root-tip cells treated as in figure 22. ×1800.

of bulbs (bulb 5) which received only 1500r showed the characteristic bending or twisting of the root-tips and fewer necrotic ones, while bulbs (bulb 18) which were colchicinized only showed outgrowths of the hypertrophied root-tips with an abundance of secondary roots. The water controls (bulb 10) showed evidence of continued growth even though bulb decay had occurred.

The roots from some bulbs selected at random from each of these series were counted and measured before and after treatment. These were removed after their return to water for 19 days to study better the effect produced by the treatment. The control bulbs grown in water for 29 days had a number of long roots with many secondaries. Some of the small roots appeared water-soaked and necrotic. The root-tips on the rest were firm and appeared to be active. The roots that were irradiated with 1500r had been in water 10 days before and 19 days after treatment. The effects of the x-rays seemed to be confined to the root-tips, where slight twisting and bending were noted. There was evidence of growth, but no secondary roots appeared. The roots which were irradiated with 3000r showed more marked distortion of the root-tips of the long roots, while the short ones showed no such evidence. The irradiated root-tips appeared viable and capable of growth. The bulbs that were colchicinized only and returned to water produced a large number of new roots with an abundance of secondary ones; these developed after the bulbs were returned to water, giving further evidence that colchicine had no permanent growth-inhibiting effect.

Roots examined from the bulbs that were colchicinized and irradiated with 1500r 19 days after treatment showed a very limited extension of the bulbous tip on a few of the roots. Here the inhibition of growth induced by colchicine and x-rays was practically complete. Similar gross effects were obtained with longer exposures to colchicine (72 hours) and less irradiation (900r). Roots of colchicinized bulbs irradiated with 3000r were completely arrested in growth. A number of the roots were water-soaked and necrotic. No new roots were formed and no secondary roots were visible. The x-ray dosage which completely inhibits growth seems to be slightly above 1500r when combined with an exposure to 0.01 per cent colchicine solution for 48 hours.

It appears that the 48-hour-colchicinized bulbs were more vulnerable to the x-ray treatment even though the time of exposure occurred when the number of dividing cells had passed the peak of their reaction to the drug. The "colchicine tumor" furnished a means of demonstrating growth inhibition and helped to point out clearly that the colchicine facilitated the action of the x-rays in permanently arresting growth and destroying tissue. Microscopic studies of these roots together with daily measurements furnished further evidence on this point.

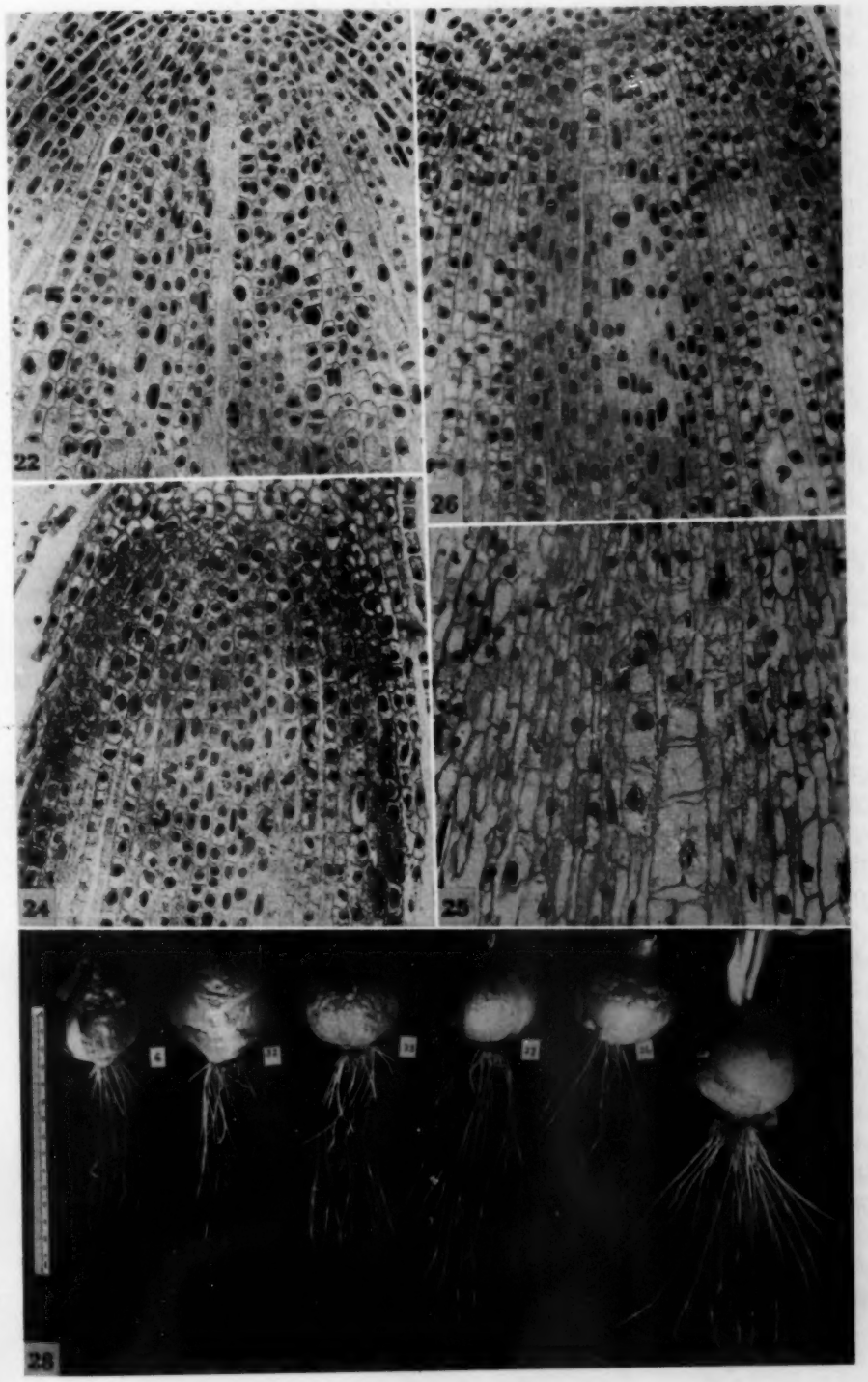
CYTOLOGICAL CHANGES INDUCED WITH 1500R OR 3000R

Microscopic studies of the root-tips of the "Brigham Yellow Globe" variety were made before and at various periods after exposure to colchicine. The root-tips fixed in this series from samplings taken from all bulbs before treatment showed abundant karyokinetic activity. In root-tips exposed to colchicine for six hours there was an accumulation of metaphases in which the chromosome masses seemed to be radiomimetic. The cells in the dermatogen were deeply stained and poorly differentiated. The root-tips exposed for 12, 18, 24, and 48 hours contained an increasing number of metaphases except in the last group. Root-tips of this variety of onion colchicinized for 48 hours and studied 24 hours after their return to water recovered from the colchicine effect (fig. 22). Characteristic giant cells with lobulate nuclei and normal nuclear and cell divisions were found. The hypertrophy of the root-tips was marked, yet the cells were definitely oriented in regular tiers as shown in this section and described earlier by Levan (1938), Shimamura (1939a), Mangenot (1939), and others. Yet many of the sections seemed aberrant because of the difference in size of the cells. The cell arrangement, however, was so regular that no analogy between this hypertrophy and the crown-gall disease or malignant growths of animals could be made. The "colchicine tumor" does not fall into any category of tumor growth.

It has been shown by Levan (1938) and others that polyploidy occurs in colchicine-treated root-tips, and large numbers of chromosomes have been counted. Increasingly large masses of distinct, clearly differentiated, apparently normal chromosomes were observed in the cells of the same root-tip (fig. 23). Polyploid cells were frequently found in these "colchicine tumors," in crown-gall, and in tumors of animal and man (Levine 1931). Polyploidy does not appear to be the sole criterion for malignancy. The causes of this increased chromosome-number in overgrowths are not known, though it may be ascribed to some disturbance in the spindle mechanism. It appears that in the polyploid cells of colchicine-treated root-tips the chromosomes may separate in anaphase regularly and equally. The reconstructed nuclei, although sometimes lobulate, go through a normal mitosis when the influence of the drug is removed. The radiomimetic effect induced by the colchicine disappears. Isolated chromosome masses may be reconstructed to form small or irregularly shaped nuclei which account for the irregularity in the size of the cells. These features are constant characteristics of malignant growths and

Explanation of figures 22, 24–26, 28

FIG. 22. Root-tip colchicinized 48 hours; fixed after 24 hours in water. × 250. FIG. 24. Root-tip exposed to 1500r; fixed 120 hours after treatment. × 250. FIG. 25. Root-tip exposed to colchicine for 48 hours; irradiation 1500r; fixed from water 120 hours later. × 250. FIG. 26. Root-tip exposed to colchicine for 48 hours, irradiation 3000r; fixed from water 24 hours later. × 250. FIG. 28. Bulbs exposed to colchicine for 18½ hours followed by irradiation with 1500r; 9 days after return to water. Bulbs 26, 27, 28, colchicine and x-rays; 30, colchicine; bulbs 6 and 32, x-rays. × 0.6.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are consistently perpetuated in these growths, while in the colchicine-treated tissue the normal and polyploid cells seem to persist in subsequent cell generation and assume normal behavior under normal conditions.

Non-Colchicinized Irradiated Roots. Normal roots irradiated with 1500r and returned to water for 24 hours contained no nuclear division figures as observed by Sax (1941). The peripheral cells of the root-tips were densely stained and the contracted nuclei appeared to be in the resting stage. Irradiated root-tips taken from the same bulbs 120 hours after their return to water resumed growth, as witnessed by the number of division stages (fig. 24). The resting nuclei appeared normal, yet some had more than two nucleoli. The nuclei had assumed a central position in the cell and the nucleoli appeared to be isolated by a clear area of nucleoplasm. Macroscopically the roots appeared normal.

Colchicinized for 48 hours with 1500r or 3000r. Root-tips colchicinized for 48 hours and then irradiated with 1500r, and returned to water for 120 hours, showed (fig. 25) elongated old cells with large contracted, undifferentiated nuclei, from which cytoplasmic strands radiated. Here obviously, the colchicine effect has been augmented by the injurious influence of the x-rays. Control roots irradiated with 3000r and examined 24 hours later contained no division figures. The nuclei, in the dermatogen and outer layers of the periblem somewhat irregular in outline, appeared as densely stained undifferentiated bodies. The plerome and inner layers of the periblem had a well differentiated cellular structure. The root-tips colchicinized for 48 hours, irradiated with 3000r, and examined 24 hours after their return to water were also lacking in division stages (fig. 26). The cells in the periblem and plerome had many contracted nuclei which were heavily stained. The nuclei in the peripheral cells of the root-tips appeared densely stained. Root-tips from this series examined 120 hours after their irradiation showed marked destruction of the peripheral cells (fig. 27). The calyptrogen was represented by a few elongated enucleated cells. The periblem showed contracted densely staining nuclei with little cytoplasm. The pericycle about the plerome formed regular tiers of cells in which the nuclei were densely stained and undifferentiated. Some of these cells, however, had a granular densely stained cytoplasm while still others appeared to be considerably plasmolyzed. The plerome had formed a number of layers of cells in which poorly differentiated nuclei were present. The cytoplasm was sparse and the vacuoles large. No division figures were found in any of the numerous serial sections made of these roots. It was obvious that these roots had been severely damaged, although the early development of this injury was not visible.

This microscopic study shows rather conclusively that the combined effects of colchicine and x-rays are more effective in reducing the rate of growth and bring about earlier necrosis under the conditions of these experi-

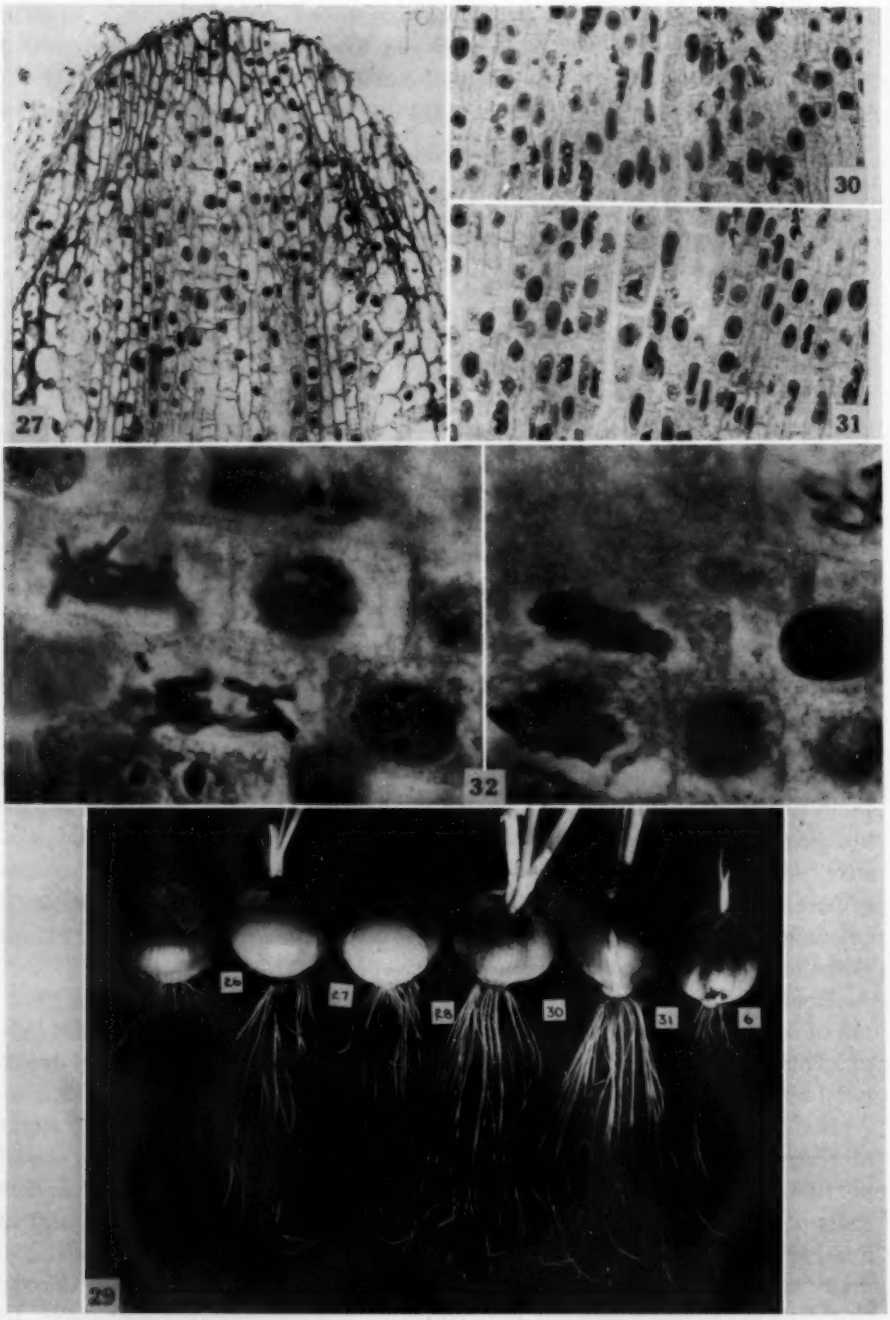
ments than x-rays alone. No root markings were successfully made to show the difference in effect produced by the x-rays on normal and colchicinized root-tips. However, the cytological evidence and a study of the growth of the root-tips (tables 5, 6) under various treatments show that the colchicinized root-tips are more vulnerable to x-rays than those non-colchicinized.

EFFECT OF SHORT EXPOSURES TO COLCHICINE

The fact that in onion root-tips exposed to colchicine for 48 hours irradiation with 900r or 1500r retarded and inhibited the outgrowths of the colchicine hypertrophies made it necessary to study the effects of irradiation on roots exposed to this substance for some periods shorter than and intermediate between 24 and 48 hours. Eighteen onions of the "Yellow Globe" variety were germinated in tap water for eight days and then exposed to 0.01 per cent solution of colchicine for 18½ and 36 hours to test the effect of x-irradiation of 1500r. A six-hour exposure to colchicine seemed too short to bring about the necessary toxic effects; while nuclear divisions were arrested and metaphases began to accumulate, no hypertrophies were produced and root measurements were necesary to determine the effect produced.

Fourteen bulbs were set in the colchicine solution. After 18½ hours a group of seven designated as "A" was returned to water. The remaining seven bulbs, group "B," were continued in colchicine for 17½ hours longer. At the end of 18½ and 36 hours, five bulbs from each group were irradiated with 1500r, and two bulbs not colchicinized were irradiated with each group. Photographic records were made at frequent intervals after they were returned to water. The colchicinized and x-rayed root-tips, nine days after their return to water (fig. 28, bulbs 26, 27, 28) resumed growth from the bulbous tips. The hypertrophies were small after this short colchicine exposure, nevertheless, they were recognizable and marked clearly the new growth after their return to water. When contrasted with the non-irradiated colchicinized roots (fig. 28, bulb 30) little or no difference was noted, except that the latter produced many secondary roots.

Root-tips irradiated only (fig. 28, bulbs 6, 32) showed only slight twisting of some of the root-tips. Those colchicinized and irradiated were not permanently affected in their ability to resume growth, yet 23 days after treatment these bulbs (fig. 29) presented some contrast with the earlier stages. At this time colchicinized-x-rayed bulbs (bulbs 26, 27, 28) showed only slight increases in the length of roots. Secondary roots were formed on the distal portion of some of the long primaries and some new roots had formed. The roots of the x-rayed bulbs (bulb 6) had increased slightly in length and in number. The colchicinized non-irradiated bulbs (bulbs 30, 31) produced many new roots, as well as long outgrowths from the hypertrophied root-tips. The colchicine appeared to produce no marked observable changes. In contrast with these results the longer colchicine exposures, 48 hours and



. FIG. 27. As in figure 26; fixed 120 hours after irradiation. ×250. FIG. 29. Same as figure 28; 23 days after return to water. ×0.6. FIG. 30. Section of root-tip colchicinized 18½ hours. ×500. FIG. 31. Section of root-tip in colchicine for 18½ hours, irradiation 1500r. ×500. FIG. 32. Chromosomes and resting nuclei in root-tips as affected by colchicine and irradiation; treatment as in figure 31. ×1800.

more, followed by 1500r brought about nearly complete and permanent inhibition of growth.

Microscopic sections were studied of roots taken from bulbs 26, 27, and 28 after 18½ hours exposure to colchicine and immediate fixing. The metaphase stages (fig. 30) were in abundance and confined principally to the periblem and dermatogen. Here many early prophases appeared and indicated marked growth activity. Sections of fixed material made 24 hours after the colchicine treatment showed normal cells, some of which were in prophase and telophase stages; while those root-tips which were colchicinized, irradiated, and immediately fixed showed the intensified clumping of chromosomes commonly seen in the primary stages of x-ray effects referred to above (fig. 31). The resting nuclei in some of the cells (fig. 32) showed the characteristic clear area about the nucleoli. The dividing nuclei consisted of longitudinally split chromosomes, chromosome fusions, and in some instances fragmentation.

It seems that while colchicine causes analogous cytological changes at 6, 12, 18, 24, and 48 hours of exposure, the longer exposures induce some microscopically unrecognizable alterations. These changes permit the cells to resume growth for a short period after the shorter exposures to colchicine followed by 1500r, but completely and permanently arrest the growth when the longer colchicine exposures are followed by the same x-ray dosage. This is evidence of the fact that the irradiation is not the sole factor that inhibits growth but that both agents supplement each other effectively.

In the colchicinized-irradiated root-tips 24 hours after treatment no division figures were found. The nuclei appeared to be contracted, yet beautifully differentiated with ruby-red bodies, apparently nucleoli, and numerous granules stained with gentian violet on a delicate reticulum. The nuclei appeared somewhat irregular in shape and resembled those described above.

Root-tips of bulbs irradiated only were studied immediately after the roots were irradiated with 1500r. The cytological changes of the division figures were less marked than in the colchicinized-x-rayed root-tips. Many of the resting nuclei were heavily stained. In the resting nuclei the chromatic material was concentrated near the nuclear membrane, leaving a clear area about the nucleoli. Some of the peripheral cells contained densely stained undifferentiated nuclei. The cytological structure of the root-tips fixed 24 hours after irradiation was normal but no division figures were seen. The arrangement of the chromatic material about the nuclear membrane was not marked but was evident in some cells.

At the end of this experiment, 31 days after irradiation, the roots of colchicinized and irradiated bulbs had increased only slightly in length. Some of the roots took on a dingy brown color. The roots which had been colchicinized only were growing vigorously, while roots that had been irradiated only had grown in an irregular manner so as to be apparently twisted at the tips.

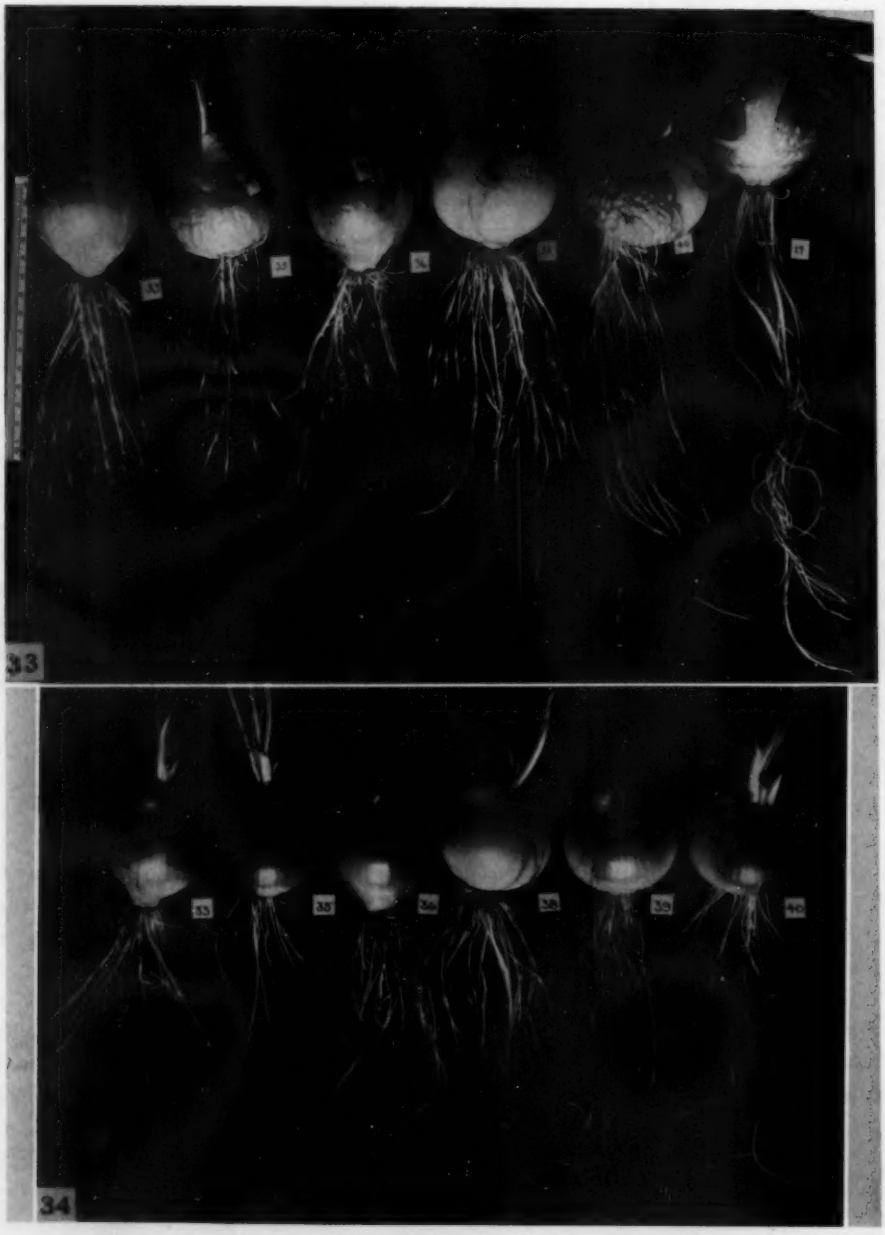


FIG. 33. Bulbs 33, 35, 36, exposed to colchicine for 36 hours; irradiation 1500r; bulb 38, colchicine only; bulb 40, irradiated only; bulb 17, water only; 8 days after water. × 0.6. FIG. 34. Same group as figure 33, 22¼ days after their return to water; bulb 39, colchicine-treated only. × 0.6.

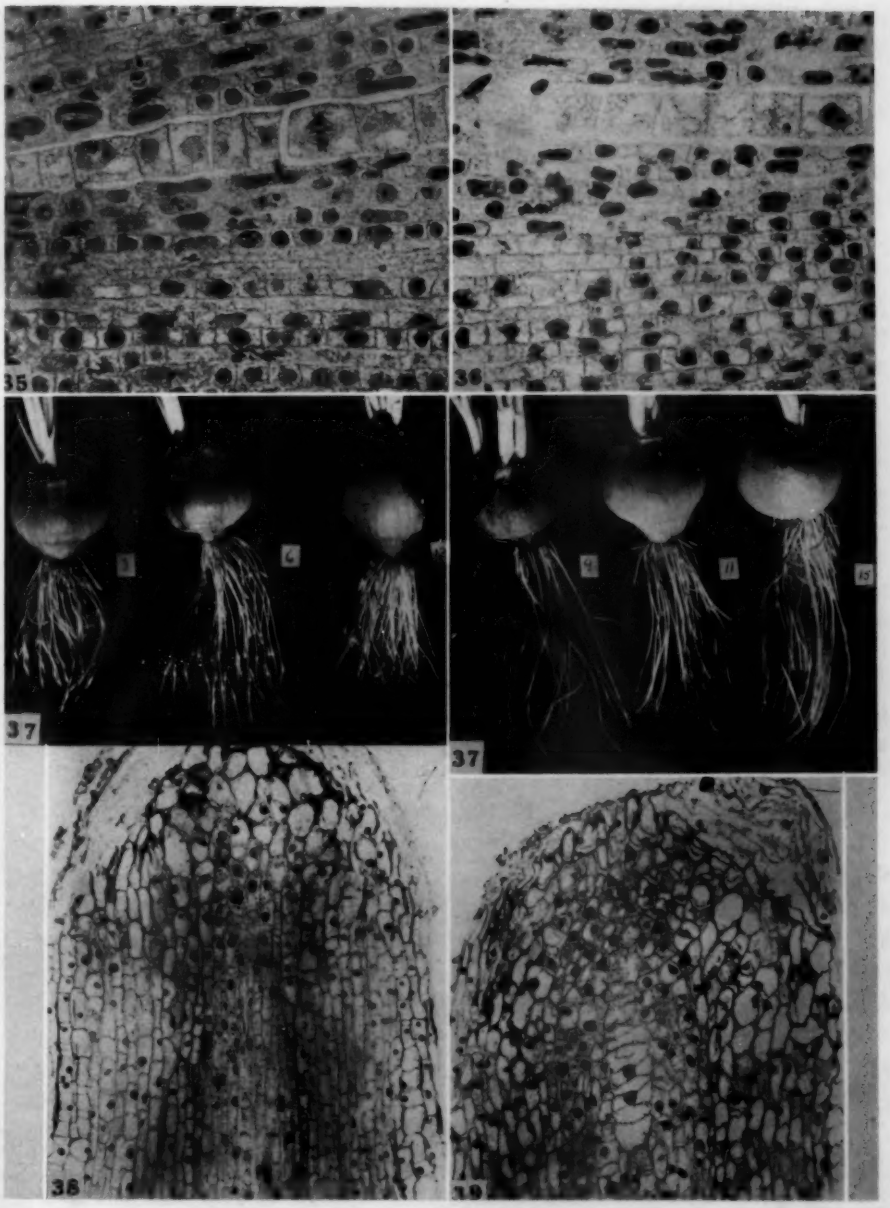


FIG. 35. Root-tip colchicinized 36 hours; fixed 24 hours after return to water. ×500. FIG. 36. Exposed to colchicine 36 hours; irradiation 1500r. ×500. FIG. 37. Bulb 3, colchicine 48 hours, irradiation 3000r; bulb 6, colchicine 2 days; bulb 13, irradiation 3000r, followed by water 6 days; bulb 11, acenaphthene 2 days, irradiation 3000r; bulb 9, acenaphthene 2 days, 6 days in water after treatment; bulb 15, water only. ×0.6. FIG. 38. Root-tip from bulb 11 (fig. 37) 2 weeks after irradiation. ×250. FIG. 39. Root-tip after exposure to colchicine for 48 hours; irradiation 3000r; returned to water for 2 weeks. ×250.

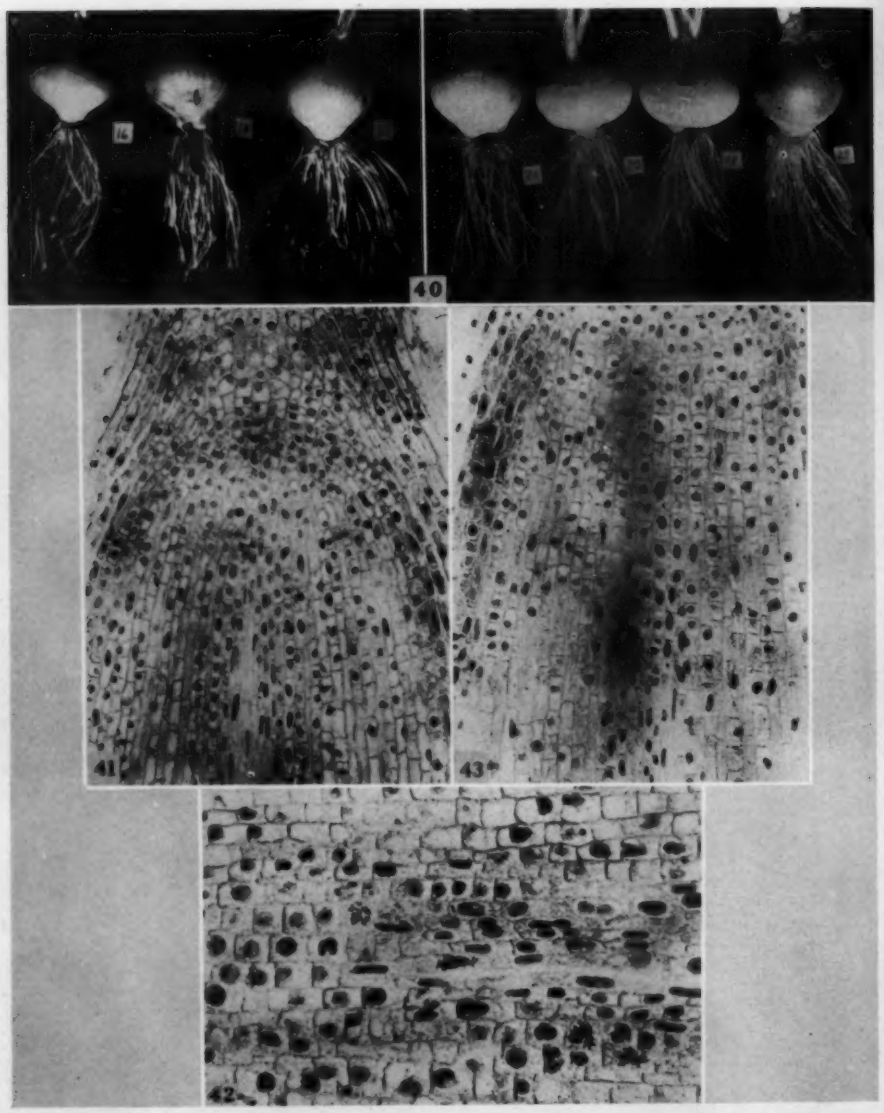


FIG. 40. Bulbs 16, 18, 21, colchicinized for 2 days, exposed to 1500r, and returned to water for 6 days; bulb 23, exposed to acenaphthene for 2 days; bulb 25, exposed to acenaphthene for 2 days, irradiation 1500r; bulb 28, irradiation 1500r; bulb 29, untreated; 7 days after their return to water. × 0.6. FIG. 41. Root-tip from bulb 28 shown in figure 40, 4 days after irradiation. × 250. FIG. 42. Root-tips from bulb treated with acenaphthene for 48 hours. × 250. FIG. 43. Root-tip from bulb treated with acenaphthene and irradiation 1500r; 4 days after the treatment. × 250.

The "B" group included onions exposed to colchicine for 36 hours followed by irradiation with 1500r. Of this group (fig. 33), bulbs 33, 35, and 36 were colchicinized and irradiated; bulb 38 was colchicinized only; while bulb 40 was irradiated only and bulb 17 was not treated. The photograph shown as figure 33 was taken eight days after treatment.

The hypertrophied tips on the colchicinized irradiated group had grown slightly 8 days after their return to water in comparison with those (bulb 38) that were colchicinized only. The bulbs irradiated only had root-tips which grew with characteristic irregularity. Twenty-two days after their return to water (fig. 34) there appeared to be little change in the length of the colchicinized-irradiated roots. There were some flaccid, water-soaked roots, while no new roots appeared. The bulbs colchicinized only showed an extensive growth from the hypertrophied root-tips. The bulbs irradiated only showed some increase in root length and some new roots appeared.

It is obvious that the effects of colchicine and irradiation are more active when combined than when used singly. The irradiated plants studied are affected, but not so much as those that received the longer colchicine treatments. It appears that the optimum effect is attained when irradiations are combined with an exposure to colchicine of more than the 36 hours. The combination of 900r with 0.01 per cent colchicine for 72 hours or 1500r with 48 hours exposure to colchicine is most effective in arresting root growth without destroying the root.

There was no marked microscopic difference between these roots and those treated for 18 hours in colchicine. Serial sections of the root-tips 24 hours after the 36-hour exposure to colchicine showed many normal as well as polyploid cells (fig. 35). The prophase division stages were abundant; anaphase cells which appeared polyploid although not exceedingly hypertrophied were found here with numbers of contracted chromosomes. The colchicinized-irradiated root-tips (fig. 36) contained many resting cells which were densely stained. There was evidence of contraction of the chromatic network. The dividing nuclei had the chromosomal fusions typical of colchicine-irradiation treatments, which appeared to be somewhat more intense than the radiomimetic effects of colchicine alone. Of these bulbs, root-tips examined 24 hours after irradiation had no division figures, and the cells resembled those observed in the 18-hour colchicine irradiation group.

It appears that the longer colchicine exposures induced some non-recognizable toxic change, which makes the cells more susceptible to the irradiation. The fact that the greatest x-ray effect is induced after exposures to colchicine for more than 48 hours indicates that the action of the x-rays is independent of the nuclear division phase but is in some way dependent upon the influence exerted by the colchicine.

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MEDICINAL HERBACEOUS SPECIES IN THE NORTH-EASTERN UNITED STATES

RALPH HOLT CHENEY

Economic botany, particularly in its food and materia medica phases (Godshall 1942; Merrill 1943), served the war effort directly in numerous ways. This paper is limited to those vascular plants which are potential sources of drugs in the northeastern part of the United States. These plants are of interest because they could be gathered annually to supply a part of the total amount of the therapeutic compounds used by the medical profession. Some of these botanic drugs are important medicinal agents and are not made synthetically. These species could also provide the basis for the establishment and subsequent genetic improvement of a cultivated crop not produced currently in the area surveyed. A considerable list of drug plants such as described by the author and others (Ballard, Cheney & Pokorny 1943) for the Brooklyn Botanic Garden, are displayed usually in municipal and institutional botanical gardens. In every such display, however, the number of individual plants of most of the species is so small that they could not serve effectively as a source of seeds or other parts for any extensive propagation of a drug crop. Even before the present world war, a Committee on Pharmacognosy and Pharmaceutical Botany of the National Research Council began an investigation[1] of the wild medicinal plants of the United States. One of the purposes of this survey was to tabulate the geographic distribution and abundance of naturally growing domestic sources of botanic drugs for reference in periods of national emergency. Although considerable data on the location, abundance, and some useful ecological information, had been compiled by the advent of the United States into the war, it was obvious that the magnitude of this task would make its value primarily one of a long term nature.

Early in 1941, it was my privilege to discuss, before the combined committees of the New York Academy of Medicine, the problem of drug plant sources and their availability in view of the drug shortages due to the effect of the war upon our normal importation. During the next two years some of the commercial companies increased their acreage of drug plants as much as one thousand per cent. The Federal Government has grown quinine seed-

[1] "A Survey of the Wild Medicinal Plants of the United States—Their Distribution and Abundance 1937; with supplements. Compiled by the Committee on Pharmacognosy and Pharmaceutical Botany, Division of Biology and Agriculture, National Research Council. (Processed. Not for general distribution.)"

lings (Cinchona varieties of the cultivated Dutch East Netherlands type) and distributed them for planting in proper ecological areas of tropical America. Moreover, the U. S. Cinchona Mission to South America reports (Steere 1945), in addition to the common quinine-producing species, an area in southern Colombia and Ecuador where the supposedly rare species, *Cinchona pitayensis,* is fairly abundant. Its bark yields 3% quinine sulphate. In addition, this mission reports the bark of another small tree, *Remijia pedunculata,* although not the genus *Cinchona,* also yields 3% quinine sulphate and is abundant in the eastern range of the Colombian Andes. Already the *Cinchona* bark quotas set up in 1942 by the U. S. Office of Foreign Economic Administration in an arrangement with the Andean governments have been exceeded. The Bureau of Plant Industry, cooperating with the Bureau of Narcotics, has information for the production of opium and suitable seeds to meet the morphine requirements of both the military and civilian needs of the U. S. (Sonnedecker 1943). Our northwestern States can supply, if commercial growers should fail, enough *Digitalis purpurea* L., to supply our demand.

The author began an investigation in 1941 to determine the availability of herbaceous medicinal species occurring in the wild state and in nurseries, in the northeastern area of the United States. In spite of considerable field data on hand, it was impossible to tabulate in any great detail the local distribution of wild and cultivated medicinal species. Moreover, the literature reveals no standardized criteria for the determination of drug plant species, especially when non-official species were included. Therefore, it was decided that the study would attempt merely to *list* the herbaceous medicinal species in the area surveyed and to obtain *quantitative* data only on ten representative drug plants known to be utilized in current pharmaceutical preparations. The author (Cheney 1944) has made a preliminary report on these ten species, which were chosen from a list (Gathercoal 1941, 1942) involving a wide variety of therapeutic principles and plants typical of the several major ecological conditions existing within the area surveyed. Since these ten species were cultivated, their abundance in the approximating 2400 nurseries of the States involved indicated their availability for medical utilization during the present emergency. The eight States involved are New Jersey, New York, Connecticut, Rhode Island, Massachusetts, Vermont, New Hampshire, and Maine. During the past four years, the majority of the nurseries which grow herbaceous plants, have been visited by the author in connection with his field trips or information was obtained by questionnaire. The ten selected drugs, with the species from which they are obtained, are shown in the accompanying table.

The wild herbaceous, medicinal species occurring in the northeastern area include actual and potential sources mostly of minor therapeutic signifi-

Botanical Origin	*Common Name*	*Part Used*	*Drug Name*	*Drug Status*[a]	*Medicinal Use*[b]
Aconitum napellus L.	Aconite or monkshood	Tuberous root	Aconitum	O	Cardiac & respiratory depressant, anodyne, antipyretic
Aloe vera L. (*Aloe barbadensis* Miller)	Barbadoes aloes or bitter aloe, Curaco aloe	Inspissated and dried leaf juice	Formerly Aloe & aloin Now Aloinum[c]	O	Cathartic, improve healing rate from X-ray burns
Atropa belladonna L.	Belladonna or deadly nightshade	Leaves & roots alkaloid	Formerly Belladonnae Radix & Belladonnae Folium. Now is Atropina	O	Anodyne, mydriatic, decreases secretions, relaxes smooth muscle in asthmatic spasms
Convallaria majalis L.	Lily-of-the-valley	Rhizomes & roots[d]	Convallaria	O	Cardiac stimulant, diuretic properties similar to digitalis but non-cumulative
Datura stramonium L.	Jimson weed or Jamestown weed	Dried leaves & flowering tops	Stramonium	O	Similar properties to Belladonna, dilates bronchioles in Asthma
Digitalis purpurea L.	Purple foxglove	Dried leaves	Digitalis folium or Foxglove	O	Cardiac stimulant, diuretic
Hyoscyamus niger L.	Black henbane	Dried leaves with or without tops	Hyoscyami folium or Henbane	O	Similar to Belladonna but chiefly a sedative in inflammatory conditions of genito-urinary tract, checks vesical spasm in urinary incontinence
Salvia officinalis L.	Garden sage	Dried leaves	Salvia or Sage	O	Condiment & carminative in flatulence
Urginea maritima (L.) Baker	Squill or sea onion	Bulb	White or Mediterranean squill or Scilla	O	White variety emetic, a nauseant expectorant in small doses & a cardiac drug in large doses
		Inner scales of bulb	Red variety	U	Red variety is emetic & rodenticide. (Rats cannot regurgitate)
Valeriana officinalis L.	Common or garden valerian	Rhizomes & roots	Valeriana	O	Supposed nervine, carminative, anti-hysteric, anti-spasmodic

[a] O = official; U = unofficial.

[b] The author wishes to acknowledge with grateful appreciation, the assistance of Benjamin L. Milana of the department of Materia Medica, Brooklyn College of Pharmacy, Long Island University, in the preparation of the data cited under Medicinal Use.

[c] Mixture of bitter pentosides, not an alkaloid.

[d] Flowers (& leaves) also have physiological action. They are unofficial as Convallariae flores.

cance. If not of major medicinal value, they are of interest from the viewpoint of their availability for plant breeding. The concentration of active therapeutic compounds can be accomplished as it has been done with *Aconitum* (Bonisteel 1943). The data presented should be of importance, not only for their possible collection for emergency utilization, but because they are elucidative on the possibility of developing certain species as the basis of a future drug source industry in this area which would protect us against shortages in the event of similar national emergencies.

The wild herbaceous species possessing medicinal value and growing naturally in general throughout the eight states—unless otherwise indicated—covered by this survey are shown in the table on pp. 64–70.

SUMMARY

With the exception of considerable numbers of plants of *Convallaria*, only a relatively few plants or a small quantity of seed is available of the ten cultivated species. One or more of these species is propagated by the growers of several states only to the following extent: in 14 per cent of the Connecticut nurseries, Maine 0, Massachusetts 40 per cent, New Hampshire 30 per cent, New Jersey 20 per cent, New York 20 per cent, Rhode Island 28 per cent, and Vermont 24 per cent. These percentages would be reduced very greatly if it were not for the inclusion of lily-of-the-valley and sage in this list. By less than 0.5 per cent of the nurseries a few plants were reported of *Atropa belladonna* L. (belladonna), *Colchicum autumnale* L. (colchicine), *Hedeoma pulegioides* (L.) Pers. (American pennyroyal), and *Urginea maritima* (L.) Baker (red squill). A more informative picture of the scarcity of the drug plant propagation of these ten species for which quantitative data were obtained may be shown by the tabulation cited below for the area surveyed.

Species	Conn.	Me.	Mass.	N.H.	N.J.	N.Y.	R.I.	Vt.
	per cent nurseries in which grown							
Aconitum napellus L.[a]	0	0	5%	5%	4%	12%	1%	8%
Aloe vera L.	0	0	0	0	0	0	0	0
Atropa belladonna L.	0	0	0	0	0.5%	0	0	0
Convallaria majalis L.	14%	0	40%	12%	12%	20%	2%	12%
Datura stramonium L.	0	0	0.5%	0	0	0.5%	0	0
Digitalis purpurea L.	0.5%	0	5%	5%	8%	8%	2%	1%
Hyoscyamus niger L.	0	0	0	0	0	0	0	0
Salvia officinalis L.	0.5%	0	30%	2.5%	8%	4%	1%	12%
Urginea maritima (L.) Baker	0	0	0	0	0	0	0	0
Valeriana officinalis L.	0.5%	0	20%	2.5%	12%	8%	2%	1%

[a] Much of the aconite was found to be *A. Fisherii*, not *A. napellus* L.

The *cultivation* of drug plant species by a few botanic drug companies has increased greatly since the advent of world war II. Otherwise, in com-

[b] The author wishes to acknowledge with grateful appreciation, the assistance of Benjamin L. Miliana of the department of Materia Medica, Brooklyn College of Pharmacy, Long Island University, in the preparation of the data cited under Medicinal Use.

[c] Mixture of bitter pentosides, not an alkaloid.

[d] Flowers (& leaves) also have physiological action. They are unofficial as Convallariae flores.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*[a]	*Medicinal Use*
Acorus calamus L.	Sweet flag; marshes of lower altitudes	Peeled rhizome	Calamus	O	Carminative, aromatic bitter as stomachic stimulant
Agropyron repens (L.) Beauv.	Couch or dog-grass; fields & waste places	Rhizome & roots	Triticum	O	Demulcent, diuretic
Apocynum cannabinum L. var. *hypericifolium* (Ait.) Gray	Indian or Canadian hemp; moist banks with gravelly or sandy soil	Rhizome & roots	Apocynum	O	Cardiac stimulant (poison), (contains glucosides), diuretic
Aralia nudicaulis L.	Wild sarsaparilla; moist woodlands	Aromatic roots	Substitute for true Sarsaparilla	U	Alterative (Substitute for official Sarsaparilla)
Aralia racemosa L.	American spikenard or spignet; rich woodlands	Rhizome & roots	Aralia or spikenard	O	Alterative
Asarum canadense L.	Wild ginger or Canada snakeroot; rich rocky woods	Rhizome & roots	Asarum	O	Aromatic bitter, carminative
Caulophyllum thalictroides (L.) Michx.	Blue cohosh or papoose root; rich woods	Rhizome & roots	Caulophyllum	O	Antispasmodic, emmenagogue, oxytocic
Chelidonium majus L.	Celandine; waste places	Entire flowering plant	Chelidonium	U	Cathartic, diuretic, diaphoretic, expectorant
Chimaphila umbellata (L.) Nutt.	Pipsissewa or prince's pine; dry woods	Leaf	Chimaphila	O	Diuretic, tonic and astringent on mucous membrane of genito-urinary tract

[a] O = official; U = unofficial.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Cimicifuga racemosa (L.) Nutt.	Black snakeroot or black cohosh; rich woods (not in northern N.E. range)	Rhizome & roots	Cimicifuga	O	Antirheumatic, uterine tonic (doubtful), possibly alterative
Coptis trifolia (L.) Salisb.	Goldthread; wet woods	Entire herb	Coptis	U	Bitter tonic
Cypripedium hirsutum Mill.	Showy yellow lady's slipper; cold swamps	Rhizome & roots	Cypripedium[b]	U	Nervine, antispasmodic
Cypripedium parviflorum Salisb.	Smaller yellow lady's slipper; bogs and swampy woods	Rhizome & roots	Cypripedium[b]	U	Nervine, antispasmodic
Cypripedium pubescens Willd.	Larger yellow lady's slipper; rich moist woods	Rhizomes & roots	Cypripedium[b]	U	Nervine, antispasmodic
Delphinium ajacis L.	Larkspur; fields & wet places (not in N. H. & Maine)	Seed	Delphinium	O	Parasiticide in pediculosis
Delphinium ajacis L. Var. *alba* Cheney	White larkspur; fields locally; east. Mass. (Cheney in Rhodora, 1925)	Seed	Probably contains same alkaloid "Adjacine," $C_{34}H_{46}O_9N_2 \cdot 2H_2O$, as the species with similar properties.		
Dicentra canadensis (Goldie) Walp.	Squirrel corn; rich woods	Tubers	Corydalis or Turkey Corn	O	Alterative in chronic cutaneous affections, tonic
Dicentra cucullaria (L.) Bernh.	Dutchman's Breeches; rich wooded hillsides	Tubers	Corydalis	O	Similar to above
Drosera anglica Huds.	Sundew; marly bogs	Entire plant	Drosera or Sundew	U	In proprietary remedies for bronchitis and cough

[b] Cypripedium is known also as American valerian and used as a substitute for valerian in hysteria.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Drosera longifolia L.	Sundew; bogs and sandy shores	Entire plant	Drosero or Sundew	U	Expectorant
Drosera rotundifolia L.	Round-leaved sundew; peat bogs & wet sand banks	Entire plant	Drosero or Sundew	U	Expectorant, Alcoholic extraction of this species and *Thymus vulgaris* L. is a preferred homeopathic remedy for whooping cough (pertussis)
Dryopteris Filix-mas (L.) Swartz.	Male fern; rocky woods	Rhizome & stipes	Aspidium	O	Taenicide, vermifuge
Dryopteris marginalis (L.) A. Gray	Male fern; rocky woods	Rhizome & stipes	Aspidium	U	Similar to above
Erigeron canadensis L.	Horseweed; waste places	Volatile oil of entire plant	Oleum Erigerontis	U	Oil similar to but less irritant than oil of turpentine. Diuretic, diaphoretic, styptic
Eupatorium perfoliatum L.	Thoroughwort or boneset; low grounds	Leaves & flowering tops	Eupatorium	O	Diaphoretic, febrifuge
Eupatorium purpureum L.	Joe-Pye weed or trumpet weed; low grounds [except Maine where only the variety occurs, *E. purpureum* var. *maculatum* (L.) Darl.]	Leaves & flowering tops	Swamproot	U	Astringent
Gaultheria procumbens L.	Teaberry or checkerberry or wintergreen; cool woods	Leaves	Gaultheria[c]	U	Aromatic, astringent
Geranium maculatum L.	Wild geranium or wild cranesbill; open woods and fields	Rhizome	Geranium	U	Astringent

[c] Also Synthetic oil of Gaultheria is Official under title of Methylis Salicylas and used as rubefacient, antirheumatic and flavoring agent.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Hedeoma pulegioides L. Pers.	Amer. pennyroyal; dry fields	Leaves & flowering tops	Hedeoma or Pennyroyal	U	Carminative, aromatic, emmennogogue in colic & stomach disorders. Menstrual flow stimulant
Hydrastis canadensis L.	Golden seal (not in east. N. E.); rich woods	Rhizomes & roots	Hydrastis or Golden Seal[d]	O	Bitter tonic (urinary affections) alterative for mucous membranes
Hypericum perforatum L.	St. John's-wort; fields	Entire plant[e]	Hypericum	U	Vulnerary for bruises
Inula Helenium L.	Elecampane; roadsides and damp pastures	Rhizomes & roots	Inula	U	Diuretic, expectorant, veterinary anticepticin pulmonary diseases
Iris versicolor L.	Blue flag; wet meadows	Rhizome	Iris versicolor or Blue Flag	O	Cathartic, diuretic
Lobelia inflata L.	Indian tobacco; dry open fields and pastures	Leaves and tops	Lobelia	O	Nauseant, antispasmodic smoked with other drugs to relieve asthma
Lycopodium clavatum L.	Common club moss; dry woods	Spores	Lycopodium	O	Water repellent and protective dusting powder
Matricaria Chamomilla L.	Wild or German chamomile; roadsides and waste places (Not in Vt. & N. H.)	Flower head	Matricaria	O	Bitter tonic, carminative
Malva neglecta Wallr. (*M. rotundifolia* L.)	Common mallow or cheeses; waste places and cultivated grounds	Leaves flowers	Malvae Folia Malvae Flores	U U	Demulcent (fruit nutrient), emollient

[d] Also called Hydrastidis rhizoma P.I.

[e] Said to be injurious to browsing cattle due to the photosensitizing principle, hypericin.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Mentha piperita L.	Peppermint; moist places	Leaves & tops	Mentha piperita or Peppermint[f]	O	Carminative, flavoring agent, decreases HCl secretion (relief in peptic ulcer)
Mentha spicata L.	Spearmint; moist places	Leaves & tops. Volatile oil from fresh aerial parts of flowering plant	Mentha viridis or Spearmint Oleum Menthae Piperitae	O O	Carminative flavoring agent The same
Menyanthes trifoliata L.	Buckbean or bogbean; Sphagnum bogs and shallow water	Leaves	Menyanthes	U	Simple Bitter
Mitchella repens L.	Partridge berry or squaw vine; cool, dry woods	Entire plant	Mitchella	O	Diuretic, astringent, menstrual disorders
Nepeta cataria L.	Catnip; dry pastures	Leaves and flowering tops	Cataria or Catnip	O	Carminative, or combined with Fennel as a pacifier for infants
Panax quinquefolium L.	Ginseng; rich cool woods	Root	Ginseng	U	Aromatic bitter
Podophyllum peltatum L.	May apple or mandrake; rich woods (west. N.E. and southward)	Rhizome & roots	Podophyllum or May apple	O	Drastic or hydragogue cathartic
Polygala senega L.	Seneca snakeroot; rocky soil in northern part of N.E.	Root	Senega	O	Nauseant expectorant
Rosa canina L.	Dog rose; casual escape in Mass., R. I., Conn., N. Y., N. J., of area studied	Spurious fruit	Rosa Canina	U	Refrigerant, Astringent

[f] Menthol derived from Oil of Peppermint is Official. Somewhat antiseptic and used locally with rubefacient, analgesic, cooling & antipyretic effects.

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Rubus allegheniensis Porter	Blackberry; dry open thickets and recent clearings	Bark of rhizome & roots	Rubus	U	Astringent in diarrhoeal conditions
Rubus canadensis L.	Blackberry; moist, rocky thickets of mts. and hills	Bark of rhizome & roots	Rubus	U	Astringent in diarrhoea
Rubus idaeus L.	Red raspberry; thickets	Fresh ripe fruit, expressed juice	Rubus idaeus, liquid known as Succus Rubi Idaei	O	Flavoring agent for refrigerant drinks & medicinal preparations
Rubus occidentalis L.	Black raspberry or thimbleberry; fence rows & rich shady slopes	Bark of rhizome & roots	Rubus	U	Astringent in diarrhoea, antispasmodic (uterus)
Rubus strigosus Michx. (*R. idaeus* L. Var. *aculeatissimus* C. A. Mey. Regel & Tiling.)	Wild red raspberry; thickets & hills	Fresh ripe fruit, expressed juice	Rubus idaeus, liquid known as Succus Rubi Idaei	O	Flavoring agent for refrigerant drinks & medicinal preparations
Rumex crispus L.	Yellow dock; fields, waste, & cultivated places	Root	Rumex	U	Purgative with secondary astringent action
Rumex obtusifolius L.	Bitter dock; fields & roadside ditches	Root	Rumex	U	Similar to above. Both sometimes used in diarrhoea
Sanguinaria canadensis L.	Bloodroot; open, rich woods	Rhizome	Sanguinaria	O	Nauseant expectorant due to local irritant properties
Senecio aureus L.	Golden ragwort or life root; wet meadows & swamps	Entire plant	Senecio	U	In large doses a stimulant followed by depressant action on spinal cord & medulla
Solanum Dulcamara L.	Bittersweet; moist banks	Twigs & stems	Dulcamara	U	Sedative, anodyne, narcotic, alterative & resolvent in skin conditions
Symplocarpus foetidus (L.) Nutt.	Skunk cabbage; bogs & moist ground	Rhizome & roots	Skunk Cabbage	U	Antispasmodic, emetic (bronchial affections) salve for ringworm & rheumatism

Botanical Origin	*Common Name and Habitat in Northeastern United States*	*Part Used*	*Drug Name*	*Drug Status*	*Medicinal Use*
Taraxacum officinale Weber	Dandelion; pastures & fields	Rhizome & roots	Taraxacum	O	Simple bitter tonic; large doses laxative
Trifolium pratense L.	Red clover; fields & meadows	Inflorescence	Trifolium	O	Alterative, sedative in whooping cough
Trillium erectum L.	Wake robin or trillium; rich woods	Rhizome & roots	Trillium	O	Antispasmodic (uterus), emetic, alterative, astringent
Tussilago Farfara L.	Coltsfoot; moist clay banks & along mt. streams	Leaves	Farfara	U	Demulcent, alterative (coughs & colds)
Thymus Serpyllum L.	Creeping or wild thyme; old fields	Leaves & flowering tops	Serpyllum or Wild Thyme	U	Antispasmodic in whooping cough, asthma, & other respiratory conditions
Valeriana officinalis L.	Garden heliotrope; roadsides & thickets, escaped from cultivation	Rhizome & roots	Valeriana	O	Supposed antihysteric in nervousness, perhaps only a malodorous carminative
Veratrum viride Ait.	Amer. white hellebore; wet meadows & swamps	Rhizome & roots	Veratrum Viride	O	Vasomotor depressant to retard excessive cardiac action
Verbascum Thapsus L.	Common mullein; fields, rocky or gravelly banks	Leaves	Verbasci Folia	U	Demulcent, emollient
Verbascum phlomoides L.	Similar but only in local limited areas	Corolla with stamens	Verbasci Flores	U	Demulcent tea in combination with other ingredients rich in mucilage
Verbena hastata L.	Blue vervain; damp ground & roadsides at lower altitudes	Overground portion	Verbena	U	Expectorant & diaphoretic in form of a hot tea

parison with published historical data (Sievers 1940), the propagation acreage of drug plants in the northeastern United States has decreased decidedly since world war I. For example, in 1918 four growers in New Jersey raised belladonna on approximately 35 acres, whereas the acreage devoted to this species in 1941 was practically nil. Owing to current labor conditions, less than 25 per cent of the nurseries expressed their willingness to grow drug plants even with federal aid. However, in the spring of 1942, the United States Department of Agriculture distributed seed, and in the fall of 1942 between 400 and 500 acres of belladonna were harvested in Wisconsin, Pennsylvania, Virginia, Tennessee, Ohio, and in some states outside the northeastern area.

The wild species of this area involve 51 genera and 67 species. They are all Angiospermae with the exception of 2 genera and 3 species. They have not been utilized effectively in the present emergency. In Maine, no recent cultivation of drug plants has been attempted, but a few individuals have collected with profit such items as juniper berries and lycopodium spores. The natural resources of the other States have not been drawn upon to make any contribution to emergency drug sources. Significant quantities of some of these wild species could be gathered upon request by the medical or pharmaceutical profession for a single season. However, any annual production basis would require cultivated acreages and a concentration of the active principles by selection and breeding.

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STUDIES ON PHILIPPINE CHLOROPHYCEAE—II. SURVEY OF LITERATURE AND LIST OF RECORDED SPECIES PRIOR TO 1940

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Although the first list of Philippine marine algae was published a little more than a century ago, the number of papers or books that refer to them since that time is surprisingly small. Probably the first record of a marine alga from this region is to be found in the first edition of Blanco's *Flora de Filipinas*, published in 1837. In this work Blanco described nine plants, apparently all from the island of Luzon, to which he gave names that were applicable to alga-like plants. Most of the binomials were preëxisting, but there was no citation of authorities. The descriptions that accompany the names are very general, so that for the most part they cannot be used for determining anything more than the genus to which the plants are to be referred. The difficulties of knowing the particular species with which Blanco was dealing are further increased because there is no permanent record known of the plants he studied.

Among the Thallophyta in Blanco's first edition of *Flora de Filipinas* are to be found the following: *Fucus prolifer* Blanco, *F. denticulatis* Blanco, *F. gulaman* Blanco, *Ulva umbilicalis* Blanco, *U. compressa* Blanco, *U. reticulata* Blanco, *U. intestinalis* Blanco, *Conferva littoralis* Blanco, and *C. setosa* Blanco.

The description of *Fucus prolifer* Blanco unmistakably refers to a species of *Halimeda*, but because of its incompleteness could be applied to one of at least three different species that are relatively common in the Philippines, namely *Halimeda macroloba* Decaisne, *H. Tuna* (Ellis & Solander) Lamouroux f. *platydisca* (Decaisne) Barton, or *H. discoidea* Decaisne. It is interesting to point out that all three of these were described subsequently to Blanco's original work. The plant distributed by Merrill as *Species Blancoanae No. 993*, which he thought duplicated *Fucus prolifer* Blanco, is *Halimeda macroloba* Decaisne.

The second name in the list above, *Fucus denticulatus*, is apparently a *Sargassum;* in the second edition (1845) of the *Flora de Filipinas F. denticulatus* is replaced by the name *F. natans* Blanco. *F. gulaman*, called *F. edulis* in the second edition, may be a *Gracilaria*. The plant listed as *Ulva umbilicalis* seems to be a species of *Padina*. The *Ulva compressa* of Blanco appears undoubtedly to be a species of *Enteromorpha*, and his *Ulva reticulata* does not appear to be *U. reticulata* Forsskål, but it is more likely

a species of *Hydroclathrus*, for in the description he speaks of its brown color. Blanco's *Ulva intestinalis* does seem to correspond with *U. intestinalis* Linnaeus, now known as *Enteromorpha intestinalis* (L.) Link. The last names in the list above are not marine plants, for the description of *Conferva littoralis* refers to a species of *Chara*, and *Conferva setosa* Blanco is probably not an alga, for it is reported growing from the leaves of trees and looking like the hairs of a horse. The latter may have been a species of the algal genus *Trentepohlia* or a representative of the lichen family Usneaceae.

From this list it is possible, therefore, to claim only three of the nine species as marine Chlorophyceae, being fairly certain of the identity of *Enteromorpha intestinalis* (L.) Link, and knowing only the genera of the other two with certainty (*Enteromorpha* sp. and *Halimeda* sp.).

Five years later Berkeley (1842) in his "Enumeration of fungi collected by H. Cuming in the Philippine Islands," described as a fungus under the name *Dichonema erectum* a plant that A. Gepp and E. S. Gepp later showed to be an alga, and which they named *Avrainvillea erecta* (Berkeley) A. & E. S. Gepp.

Following this by two years, a paper by Montagne (1844) dealing with the plants collected by H. Cuming in the Philippines, listed the following seven species of green algae: *Cladophora pellucida* (Hudson) Kützing, *Ulva reticulata* Forsskål, *Caulerpa taxifolia* (Vahl) C. Agardh, *C. plumaris* (Forsskål) C. Agardh, *Codium tomentosum* (Hudson) Stackhouse, *Udotea sordida* Montagne, and *Halimeda discoidea* Decaisne. In this list *Cladophora pellucida, Ulva reticulata, Caulerpa taxifolia,* and *Halimeda discoidea* are still accepted species. Of the others, *Caulerpa plumaris* is synonymous with *C. sertularioides* (Gmelin) Howe, *Codium tomentosum* is synonymous with *C. dichotomum* (Hudson) S. F. Gray, and *Udotea sordida* (described by Montagne as new in his paper) is *Avrainvillea erecta* (Berkeley) A. & E. S. Gepp.

The Chlorophyceae from the Philippines are next mentioned by G. von Martens (1866), reporting on the botany of the Prussian Expedition to East Asia, who listed the following nine species from the region of Zamboanga, Mindanao: *Chaetomorpha inflata* Kützing, *Ulva reticulata* Forsskål, *Chauvinia clavifera* Turner, *Halimeda Opuntia* (L.) Lamouroux, *H. discoidea* Decaisne, *H. cuneata* Kützing, *Valonia utricularis* Roth, *V. macrophysa* Kützing, and *Microdictyon clathratum* Martens.

Regarding the first of the preceding list, this is one of the very few reports of *Chaetomorpha inflata* since it was first described by Kützing from Java, and because Martens described it so briefly and the occurrence of the species appears to be so rare, it is to be considered a doubtful record until it can be verified. *Chauvinia clavifera* is now synonymous with *Caulerpa racemosa* (Forsskål) J. Agardh var. *clavifera* (Turner) Weber-van

Bosse. *Halimeda cuneata* Kützing (not *H. cuneata* Hering) is listed by Barton (1901) among the synonyms of *H. gracilis* Harvey. *Valonia macrophysa* is not definitely known from the Pacific or Indian Oceans, and since the report of it was not accompanied by a description the record is to be seriously questioned. *Microdictyon clathratum*, described by Martens as new, is actually *Anadyomene Leclancherii* Decaisne. Interestingly enough, this same year Gray (in his article "On *Anadyomene* and *Microdictyon*, with the description of three new allied genera," etc.) referred a specimen from the Sulu Archipelago that Harvey had sent him to *Cystodictyon Leclancherii* (Decaisne) Gray, having considered that *Anadyomene Leclancherii* Decaisne was sufficiently different from other species of *Anadyomene* to constitute the type of a new genus.

Dickie (1876), in his "Contributions to the botany of the expedition of H. M. S. 'Challenger.'—Algae, chiefly Polynesian," adds considerably to the list of Philippine marine Chlorophyceae. He lists about 47 species of algae from the Philippines and among them are the following Chlorophyceae: From the island of Mactan, opposite the Harbor of Cebu, *Halimeda Opuntia* (L.) Lamouroux, *H. macroloba* Decaisne, *Codium tomentosum* (Hudson) Stackhouse, *C. adhaerens* (Cabrera) C. Agardh, *Polyphysa spicata* Kützing, *Ulva reticulata* Forsskål; from Zamboanga, Mindanao, *Caulerpa peltata* Lamouroux, *C. clavifera* (Turner) C. Agardh, *Halimeda Tuna* Lamouroux, *Valonia utricularis* Roth, *Dictyosphaeria favulosa* (C. Agardh) Decaisne, *Ulva reticulata* Forsskål, *Cladophora mauritiana* Kützing; from Big Santa Cruz Island, opposite Zamboanga, *Caulerpa plumaris* (Forsskål) C. Agardh, *Halimeda Opuntia* (L.) Lamouroux, *Valonia fastigiata* Harvey, and *Anadyomene flabellata* Lamouroux.

The determination of the material which Dickie called *Polyphysa spicata* is incorrect, and the specimens should have been named *Halicoryne Wrightii* Harvey according to Solms-Laubach (1895) who saw the material while preparing his "Monograph of the Acetabularieae." *Caulerpa clavifera* is synonymous with *C. racemosa* var. *clavifera*, and *Dictyosphaeria favulosa* is now known as *D. cavernosa* (Forsskål) Børgesen. *Cladophora mauritiana* is known only from the Indian Ocean, except for this report from the Philippines, and the determination is therefore questionable, especially since it is not accompanied by a description. *Anadyomene flabellata* is now known as *A. stellata* (Wulfen) C. Agardh, but the writer is inclined to feel that the material here reported is more likely either *Anadyomene Wrightii* Harvey or *A. plicata* C. Agardh, both of which are common species of this region.

Just a year later Dickie (1877) published an additional paper which was entitled "Supplementary notes on algae collected by H. N. Moseley of H. M. S. 'Challenger' from various localities." In this paper he listed a

few additional species from the Philippines, and among them (from Zamboanga) is included a single marine chlorophycean, *Acetabularia Calyculus* Quoy & Gaimard.

Piccone (1886) in his *Alghe del viaggio di circumnavigazione della Vettor Pisani* listed the following Chlorophyceae from the island of Ticao, Masbate Province: *Ulva reticulata* Forsskål, *Enteromorpha flexuosa* J. Agardh, *Caulerpa laetevirens* Montagne, and *Codium tomentosum* (Hudson) Stackhouse. Of these four species *Enteromorpha flexuosa* had not been previously reported. *Caulerpa laetevirens* is synonymous with *C. racemosa* (Forsskål) J. Agardh var. *laetevirens* (Montagne) Weber-van Bosse.

From the results of the Siboga Expedition are added several more species to the list of marine Chlorophyceae from the Philippines. Barton (1901) in her monograph on "The genus *Halimeda*" reported that *Halimeda Opuntia* (L.) Lamouroux and *H. macroloba* Decaisne are found among the Siboga collections from the Sulu Archipelago. Ten years later A. Gepp and E. S. Gepp (1911) add the following seven species in the report of "The Codiaceae of the Siboga Expedition," these also being from the region of the Sulu Archipelago: *Udotea orientalis* A. & E. S. Gepp, *U. argentea* Zanardini var. *spumosa* A. & E. S. Gepp, *U. Flabellum* (Ellis & Solander) Lamouroux, *Codium difforme* Kützing, *C. ovale* Zanardini, *C. tenue* Kützing, and *C. elongatum* C. Agardh.

Mme. Weber-van Bosse (1913) in the "Liste des algues du Siboga, I" reported the following Chlorophyceae as occurring among the collections from the Sulu Archipelago in addition to the species from the Siboga Expedition mentioned in the two preceding articles: *Ulva Lactuca* L., *U. reticulata* Forsskål, *Enteromorpha crinita* (Roth) C. Agardh, *Cladophoropsis sundanensis* Reinbold, *Valonia utricularis* C. Agardh, *V. fastigiata* Harvey, *Bornetella sphaerica* Zanardini, *B. oligospora* Solms-Laubach, *Caulerpa sertularioides* (Gmelin) Howe, *C. Selago* (Turner) C. Agardh, *C. Freycinettii* (C. Agardh) Weber-van Bosse, and *C. crassifolia* (C. Agardh) J. Agardh. In the list above *C. Freycinettii* has become *C. serrulata* (Forsskål) J. Agardh *emend.* Børgesen.

In 1918 Merrill published his "Species Blancoanae," a critical revision of the Philippine species of plants described by Blanco and Llanos, and in it three species are referred to the Chlorophyceae, namely *Enteromorpha intestinalis* (L.) Link, *E. prolifera* J. Agardh, and *Halimeda Opuntia* (L.) Lamouroux. There is no reason to doubt the accuracy of the first two determinations, but the plant which Merrill distributed in the exsiccata as *Species Blancoanae No. 993* is not *Halimeda Opuntia*, but rather *H. macroloba* Decaisne.

According to the late Dr. M. A. Howe (1932), there are the following Chlorophyceae among the algae collected at Panay Island by Lieut. H. C.

Kellers, M.D., who was attached as surgeon to the Naval Eclipse Expeditions of 1929 and 1930: *Enteromorpha lingulata* J. Agardh, *Chaetomorpha Kellersii* Howe, *Caulerpa clavifera* (Turner) C. Agardh, *C. macrodisca* Decaisne, and *Acetabularia major* Martens. The plant which Howe called *Caulerpa macrodisca* is *C. peltata* Lamouroux var. *macrodisca* (Decaisne) Weber-van Bosse.

SUMMARY OF RECORDS

Following is a check-list of all Philippine marine Chlorophyceae appearing in the literature before 1940; it has been arranged systematically so that the species come under the order and family to which they belong; each species is followed by the name of the author or authors reporting it, and the name under which it was listed if that name differs from the present accepted name. When the accuracy of a determination is in doubt the specific name is preceded by a question mark; species for which the Philippines is the type locality are marked by an asterisk.

ULOTRICHALES

ULVACEAE

ENTEROMORPHA CRINITA (Roth) C. Agardh. (Weber-van Bosse, 1913.)
E. FLEXUOSA (Wulfen) J. Agardh. (Piccone, 1886.)
E. INTESTINALIS (L.) Link. (Blanco, 1837, as *Ulva intestinalis;* Merrill, 1918.)
E. LINGULATA J. Agardh. (Howe, 1932.)
E. PROLIFERA J. Agardh. (Merrill, 1918.)
ULVA LACTUCA L. (Weber-van Bosse, 1913.)
U. RETICULATA Forsskål. (Montagne, 1844; Martens, 1866; Dickie, 1876; Piccone, 1886; Weber-van Bosse, 1913.)

SIPHONOCLADALES

VALONIACEAE

DICTYOSPHAERIA CAVERNOSA (Forsskål) Børgesen. (Dickie, 1876, as *D. favulosa.*)
VALONIA FASTIGIATA Harvey. (Dickie, 1876; Weber-van Bosse, 1913.)
? V. MACROPHYSA Kützing. (Martens, 1866.)
V. UTRICULARIS Roth. (Martens, 1866; Dickie, 1876; Weber-van Bosse, 1913.)

BOODLEACEAE

CLADOPHOROPSIS SUNDANENSIS Reinbold. (Weber-van Bosse, 1913.)

ANADYOMENACEAE

ANADYOMENE LECLANCHERII Decaisne. (Martens, 1866, as *Microdictyon clathratum;* Gray, 1866, as *Cystodictyon Leclancherii.*)
? A. STELLATA (Wulfen) C. Agardh. (Dickie, 1876, as *A. flabellata.*)

CLADOPHORACEAE

? CLADOPHORA MAURITIANA Kützing. (Dickie, 1876.)
C. PELLUCIDA (Hudson) Kützing. (Montagne, 1844.)
? CHAETOMORPHA INFLATA Kützing. (Martens, 1866.)
* C. KELLERSII Howe. (Howe, 1932.)

DASYCLADALES

DASYCLADACEAE

BORNETELLA SPHAERICA (Zanardini) Solms-Laubach. (Weber-van Bosse, 1913.)
B. OLIGOSPORA Solms-Laubach. (Weber-van Bosse, 1913.)
HALICORYNE WRIGHTII Harvey. (Dickie, 1876, as *Polyphysa spicata.*)
ACETABULARIA CALYCULUS Quoy & Gaimard. (Dickie, 1877.)
A. MAJOR Martens. (Howe, 1932.)

SIPHONALES

CAULERPACEAE

CAULERPA CRASSIFOLIA (C. Agardh) J. Agardh. (Weber-van Bosse, 1913.)
C. PELTATA Lamouroux, (Dickie, 1876; Howe, 1932, as *C. macrodisca.*)
C. RACEMOSA (Forsskål) J. Agardh
var. *clavifera* (Turner) Weber-van Bosse. Martens, 1866, as *Chauvinia clavifera;* Dickie, 1876, as *Caulerpa clavifera;* Howe, 1932, as *C. clavifera.*)
var. *laetevirens* (Montagne) Weber-van Bosse. (Piccone, 1886, as *C. laetevirens.*)
C. SELAGO (Turner) C. Agardh. (Weber-van Bosse, 1913.)
C. SERRULATA (Forsskål) J. Agardh *emend.* Børgesen. (Weber-van Bosse, 1913, as *C. Freycinettii.*)
C. SERTULARIOIDES (Gmelin) Howe. (Montagne, 1842, as *C. plumaris;* Dickie, 1876, as *C. plumaris;* Weber-van Bosse, 1913.)
C. TAXIFOLIA (Vahl) C. Agardh. (Montagne, 1844.)

CODIACEAE

* AVRAINVILLEA ERECTA (Berkeley) A. & E. S. Gepp. (Berkeley, 1842, as *Dichonema erectum;* Montagne, 1844, as *Udotea sordida;* A. & E. S. Gepp, 1911.)
UDOTEA ARGENTEA Zanardini var. *spumosa* A. & E. S. Gepp. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
U. FLABELLUM (Ellis & Solander) Lamouroux. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
U. ORIENTALIS A. & E. S. Gepp. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
CODIUM ADHAERENS (Cabrera) C. Agardh. (Dickie, 1876.)
? C. DICHOTOMUM (Hudson) S. F. Gray. (Montagne, 1844, as *C. tomentosum;* Dickie, 1876, as *C. tomentosum;* Piccone, 1886, as *C. tomentosum.*)
C. DIFFORME Kützing. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
C. ELONGATUM C. Agardh. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
C. OVALE Zanardini. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
C. TENUE Kützing. (A. & E. S. Gepp, 1911; Weber-van Bosse, 1913.)
HALIMEDA DISCOIDEA Decaisne. (Montagne, 1844; Martens, 1866.)
H. GRACILIS Harvey. (Martens, 1866, as *H. cuneata* Kützing.)
H. MACROLOBA Decaisne. (Dickie, 1876; Barton, 1901; Weber-van Bosse, 1913; Merrill, 1918, as *H. Opuntia.*)
H. OPUNTIA (L.) Lamouroux. (Martens, 1866; Dickie, 1876; Barton, 1901; Weber-van Bosse, 1913.)
H. TUNA Lamouroux. (Dickie, 1876.)

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A REVIEW OF THE STATUS OF SEVERAL AMERICAN SPECIES OF DALEA

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This article is the result of a study to determine the proper scientific name for the species of *Dalea* which is native in southern Florida. At first thought, this might seem like an easy task. One should need only to consult Small's *Manual of the Southeastern Flora*, which covers all of Florida. There the name is given as *Parosela floridana* Rydberg. This binomial was proposed in 1920 for a segregate from what had previously been called *Parosela domingensis* (DC.) Millsp. (*Dalea domingensis* DC.). In his key, Rydberg (N. Am. Flora **24**: 72. 1920) used for distinguishing characteristics for *P. floridana* the shorter and denser inflorescence, the slightly winged leaf-rachis, the scarcely hooked calyx-lobes and the 9–17 leaflets of each leaf. *P. domingensis* of the West Indies, on the other hand, was said to have an inflorescence which, at least in fruit, is lax. Also the calyx-lobes were described as decidedly hooked at the apex, the leaf-rachis decidedly winged and the leaflets 5–9. On a basis of these several correlated differences, *Parosela floridana* would appear to be an amply distinct species. Since *Dalea* is a conserved name and the necessary combination for the species in that genus is lacking, one might feel justified in making the transfer, but a study of actual specimens and a review of the nomenclatural history of related species introduces complications.

First, a series of specimens from Florida exhibits a greater amount of variability in that population than Rydberg's description suggests. The inflorescence, for example, varies from very short to relatively long. The rachises of the leaves are usually winged, even if not decidedly so. On every specimen examined, at least some of the lobes of the calyx are hooked. Finally, the number of leaflets varies from as few as seven to twenty-one per leaf. All this indicates that the inexperienced student may encounter trouble in separating *P. floridana* from *P. domingensis* on a basis of morphological characteristics. The differences cited by Rydberg are too definitely stated. Actually they seem to indicate evolutionary tendencies, not completely evolved species. As a result of study of the plants of Florida alone, considerable doubt arises concerning the validity of *P. floridana* as a separate species.

Parosela domingensis, as circumscribed by Rydberg in 1920, occurs in the West Indies and northern South America. Study of a series of specimens in the herbarium of the New York Botanical Garden likewise reveals

TABLE 1. *Data showing variability of certain characteristics in populations of Dalea*

Locality	Cuba	Hispaniola	Puerto Rico	Northern South America	Peninsula of Florida
Number of specimens examined	7	2	3	4	14
Inflorescence					
lax (no. of specimens)	4	2	0	0	0
dense (no. of specimens)	3	0	3	4	14
length in cm.	0.6–4.5 (av. 1.5)	0.8–1.8 (av. 1.3)	0.6–2.5 (av. 1.5)	0.7–1.6 (av. 1.1)	0.4–2.5 (av. 1.2)
Lobes of calyx					
hooked (no. of specimens)	7	2	2	0	14
not hooked (no. of specimens)	0	0	1	4	0
length in mm.	2–4 (av. 2.6)	4–6 (av. 4.7)	2–5 (av. 3)	3–4 (av. 3.5)	1–5 (av. 3)
Leaflets (no. per leaf)	3–11 (av. 6.7)	5–15 (av. 11)	7–15 (av. 11)	7–17 (av. 12)	7–21 (av. 14)
Rachis of leaf					
winged	7	2	3	4	14
not winged	0	0	0	0	0

a degree of variability far surpassing what might be expected from Rydberg's treatment. In table 1, data are presented for several supposedly important characteristics. These are summarized for three islands in the West Indies and northern South America. For purposes of comparison, data are also included for specimens from Florida.

Study of table 1 reveals that the populations of *Parosela domingensis* vary from island to island as well as from the mainland, also that there is no decisive set of major characteristics by which the plants of Florida may be separated from those of the islands. Only slight differences distinguish the several geographical populations. Even these differences may not be so great as indicated because the small numbers of specimens examined probably do not accurately show the range of variability in the several populations. Keeping in mind the shortcomings of the data, a few tendencies may be noted. Plants from Cuba have the longest inflorescences and average the smallest number of leaflets per leaf. The lobes of the calyx are longer in plants from Hispaniola than from elsewhere. Plants from Puerto Rico resemble those from Cuba in the length of the inflorescences, but differ in having more leaflets per leaf, as do those from Hispaniola. The plants from Florida and northern South America are similar in having the largest number of leaflets per leaf, but the lobes of the calyx are at least partially hooked in plants from Florida, but are not hooked in plants from South America. Specimens from the West Indies or the American mainland can be assigned with certainty to proper geographical population only after careful study. The extremes of variation shown in table 1 are great, while the differences are relatively slight. For that reason, the writer does not regard these geographical populations as worthy of designation as species, though the tendencies in divergence are perhaps strong enough to warrant their designation as subspecies.

The relationships of *Parosela floridana* are further complicated by the occurrence in the lower Rio Grande valley and from there southward in Mexico of a population which has in recent times been called *P. humilis* or *P. thyrsiflora*. Standley, in "Trees and Shrubs of Mexico" (Contr. U. S. Nat. Herb. **23**(2) : 455. 1922) separated *P. humilis* from *P. domingensis* as follows:

Spikes, at least in fruit, lax; leaf rachis evidently winged.	*P. domingensis.*
Spikes short and dense; rachis scarcely winged.	*P. humilis.*

Small, in his *Flora of the Southeastern United States* (p. 626. 1913), separated these so-called species as follows:

Leaflets 9–13.	*Parosela domingensis.*
Leaflets 5–9.	*Parosela thyrsiflora.*

Study of a series of eight specimens from the Gulf slope of Texas and Mexico reveals the variation in this population. In number of leaflets per

leaf, these specimens exactly support Small's statement of 5–9, but already we have found a similar situation in the Cuban population with the leaflets 3–11. The inflorescences vary in length from 5 to 20 mm. Compared with specimens from elsewhere, these are not remarkably short and dense. Inflorescences of plants from northern South America and Hispaniola are shorter, and those from Puerto Rico and Florida are equally short. Thus *P. thyrsiflora* is like *P. domingensis* from Cuba in number of leaflets, but most like Puerto Rican *P. domingensis* or Floridan *P. floridana* in length of inflorescence. It is not drastically different from these other populations. For that reason, *P. thyrsiflora* seems scarcely tenable as a separate species, but perhaps sufficiently distinctive to be considered a geographical subspecies. Although Small stated the range of both *P. domingensis* and *P. thyrsiflora* to include Texas, no Texan specimens of so-called *P. domingensis* have come to the writer's attention to support this statement.

If we search through the sheets of *Dalea* (*Parosela*) in a large herbarium, we will find specimens appearing similar to *P. domingensis*, *P. floridana*, and *P. thyrsiflora* from Florida, the West Indies, the lower Rio Grande Valley in Texas, the Gulf slope of Mexico, Central America, and northern South America. This composite population has received many names, but before discussing nomenclature, we must consider several other related species. Two of these are *Psoralea scandens* and *Dalea humilis*. Miller proposed the former name in 1768 for an American plant with climbing stem and blue flowers. At the New York Botanical Garden is a photograph of what is probably the type of this species. It is attached to a sheet bearing a specimen collected by C. A. Purpus, no. 2346, at Zacuapan, State of Vera Cruz, Mexico. The plant of Purpus and *Psoralea scandens* do not appear to be the same. *P. scandens* appears more lax and vine-like, with broader, larger leaflets, also the flowers are described as blue. The specimen from Zacuapan is a small shrub. It is not vine-like and has smaller, narrower leaflets. The petals appear to be yellowish. The distributional area of *P. scandens* is unknown to the writer, neither have any specimens come to his attention. Yet, on the basis of the photograph just mentioned and the original description, this seems to be a sufficiently distinct species. It should now be called **Dalea scandens** (Miller) Clausen, comb. nov., based on *Psoradea scandens* Miller, Gardeners' Dictionary, ed. 8, *Psoralea* no. 4 (1768). The other species to be considered at this point is *Dalea humilis* G. Don. Gen. Hist. **2**: 224 (1832). This was described originally from Mexico. It is an annual with slender stems and narrow leaflets which are acute at either end. In 1847, Schauer proposed the binomial *D. inconspicua* for this species, but that name should now be assigned to synonymy under *D. humilis* G. Don. This species occurs on the Pacific slope of Mexico where it ranges from Guadalajara and Chapala to Monte Alban near Oaxaca. The altitudinal range is from 1524 to 2438 m.

Other names which perhaps should also be considered in this discussion are *Dalea microphylla* H.B.K. and *D. trichocalyx* Ulbrich. These species are both South American and poorly understood by the writer. Their relationships to the species under discussion is not clear, but probably their status will not affect the nomenclatural conclusions set forth below. Likewise, the relationships of *Dalea vulneraria* Oerst. and *Parosela occidentalis* require elucidation.

The population primarily under discussion here, the one to which *Parosela domingensis, P. floridana,* and *P. thyrsiflora* belong, includes perennials with stout stems and leaflets which are broadly oblong-elliptical and rounded or retuse at the apex. Miller, in 1768, was probably the first to apply a name to any part of this population, namely *Psoralea humilis.* In 1790, Jacquin independently proposed a name for this same species, *Psoralea emphysodes,* typified by a plant from Caracas in South America. This was said to flower in December and January and to have hairy stems and purplish or white petals. In 1793, Jacquin published a colored plate of this species, but he changed the name to *Psoralea phymatodes.* The plate shows the leaflets and stems as glandular, but not hairy. Except for the absence of pubescence, and the straight lobes of the calyx, the plant in Jacquin's illustration resembles plants from Florida and demonstrates that the plants from there and from South America belong to the same species. Macbride in 1927 (Field Mus. Pub. Bot. **4**: 102) expressed similar views regarding the relationships of *P. emphysodes.* Since Miller's epithet, *humilis,* is not available in *Dalea* because of *D. humilis* Don., Jacquins' name, *emphysodes,* should now be applied to the aggregate species, which should be designated as **Dalea emphysodes** (Jacquin) R. T. Clausen, comb. nov., based on *Psoralea emphysodes* Jacquin, Coll. **4**: 144 (1790). This is separated from related species in the following key:

A. Stems climbing, to 2 m.; flowers blue. *D. scandens.*
AA. Stems not climbing, to 1.8 m.; flowers white, pink or yellowish, becoming brownish purple. B.
B. Plants annual; stems slender, 0.5–2 mm. in diam. at base; leaflets narrowly linear or oblong-elliptical, acute at either end. *D. humilis.*
BB. Plants perennial; stems stout, 2–5 mm. in diam. at base; leaflets broadly oblong-elliptical, rounded or retuse at apex. *D. emphysodes.*

The polytypic species, *D. emphysodes,* may now be characterized as follows: Villous or glabrous, glandular-punctate perennials with stout stems to 15 dm. tall, 2–5 mm. in diam. at base; leaves alternate, pinnately compound with rachises which are more or less winged and 3–21 leaflets which are broadly oblong-elliptical, rounded or retuse at apex, 2–15 mm. long, 1–6 mm. broad; flowers in axillary and terminal racemes, 0.4–4.5 cm. long; calyces 4–8 mm. long, with lobes linear, acute, 1–6 mm. long, hooked, recurved or straight; petals 5–10 mm. long, white, pink or purplish, becoming brownish purple; stamens diadelphous, 5–7 mm. long; pistils densely villous.

Flowering time is September to May. The distributional area includes southern Florida, the lower Rio Grande Valley, the Gulf slope of Mexico and Central America, the Pacific slope of Central America in El Salvador, the Caribbean slope of northern South America, and the islands of Cuba, Hispaniola, and Puerto Rico.

Three geographical subspecies seem sufficiently isolated and differentiated to warrant recognition. These are named and characterized, after which a key is provided for their separation.

D. EMPHYSODES subsp. **emphysodes** (Jacquin) R. T. Clausen, subsp. nov. Based on *Psoralea emphysodes* Jacquin, *ibid.*, described originally from Caracas and characterized by leaves with 7–17 leaflets, averaging 12 leaflets per leaf, and short lobes of the calyx, 3–4 mm. long, which are not hooked. This subspecies occurs on the Caribbean slope of northern South America in Colombia and Venezuela at altitudes from 46–440 m., also in Puerto Rico. Synonyms are *Psoralea phymatodes* Jacquin, Ic. Plant. Rar. **3**: 1338 (1803); and *Parosela emphysodes* (Jacq.) Rydb. N. Am. Flora **24** (2): 113 (1920).

D. EMPHYSODES subsp. **domingensis** (DC.) R. T. Clausen, comb. nov. Based on *Dalea domingensis* DC. Prodr. **2**: 246 (1825) and characterized by the leaves with 5–15 leaflets, averaging 11 leaflets per leaf, and the lobes of the calyx which are 1–6 mm. long, averaging 3.5 mm. and all or partially hooked. This subspecies is known only from Hispaniola, which is the type locality, Puerto Rico, and northern Florida, where it occurs north to latitude 26° 45′ N at Palm Beach. Synonyms are *D. enneaphylla* Bert. in DC. *ibid.* (as a synonym); *Parosela domingensis* (DC.) Millsp. Field Mus. Pub. Bot. **1**: 21 (1895); and *Parosela floridana* Rydb. N. Am. Flora **24**: 114 (1920).

D. EMPHYSODES subsp. **thyrsiflora** (A. Gray) R. T. Clausen, comb. nov. Based on *Dalea thyrsiflora* A. Gray, Proc. Am. Acad. **5**: 177 (1861) and characterized by leaves with 3–11 leaflets. Subsp. *thyrsiflora* occurs in the lower Rio Grande Valley and from there southward, mostly at low altitudes along the Gulf slope of Mexico and Central America, also it occurs on the Pacific slope of Central America in El Salvador, and in Cuba. Synonyms are *Dalea domingensis* var. *paucifolia* Coult. Contr. U. S. Nat. Herb. **1**: 34 (1890); *Parosela thyrsiflora* Vail, Bull. Torrey Club **24**: 14 (1897); and *Parosela humilis* Rydberg, N. Am. Flora **24**(2): 114 (1920). Without inspection of the type, I am unable to assign to a subspecies *Psoralea humilis* Mill. Gard. Dict. ed. 8, *Psoralea* no. 7 (1768). This is the earliest specific epithet to be applied to *D. emphysodes*, but it cannot be employed under *Dalea* because of *D. humilis* G. Don.

KEY TO THE SUBSPECIES OF DALEA EMPHYSODES

A. Leaflets 5–21, averaging 11 or more. B.

B. Lobes of calyx not hooked, plants glabrous or pubescent. *D. emphysodes* subsp. *emphysodes*.

BB. At least part of lobes of calyx hooked; plants pubescent. *D. emphysodes* subsp. *domingensis*.

AA. Leaflets 3–11, averaging 7 or fewer. *D. emphysodes* subsp. *thyrsiflora*.

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FICUS TSJAHELA

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Ficus tsjahela Burm.f. is sufficiently characterized by at least two excellent illustrations and several good descriptions; but has been associated with a disproportionately large number of obvious, but sometimes uncorrected mistakes. It is the purpose of this study to rectify the mistakes, especially that in the title, to comment upon synonymous names, and to distinguish the species from others with which it has been confused.

FICUS TSJAHELA Burm.f. Fl. Ind. 227. 1768. (Spelled *Tsjakela* by Burman.)

Tsjahela Rheede, Hort. Mal. 3: 87. *pl. 64.* 1682. (Originally spelled *Tsjakela*, but corrected on p. 88.)

F. malabarica semel in anno fructifera, fructu minimo, tsjahela dicta Ray, Hist. Pl. 2: 1435. 1688. (Spelled *Tsjakela.*)

F. surattensis Hb. Garcin ex Burm.f. Fl. Ind. 227. 1768.

F. surattensis var. *malabarica, mori folio* Hb. Garcin ex Burm.f. (above).

F. venosa Ait. Hort. Kew. 3: 451. 1789. Not Willdenow.

Pella ribesioides Gaertn. Fruct. Sem. Pl. 1: 143. *pl. 28, f. 8.* 1791.

F. tsjahela Rheede ex Vahl, Enum. Pl. 2: 185. 1806. (Spelled *Tsjakela.*)

F. infectoria Willd. Sp. Pl. 4: 1137. 1806. Not Roxburgh.

F. indica Moon, Cat. Pl. Ceylon 74. 1824. Not Linnaeus.

F. sp. Hb. Heyn. ex Wall. Cat. no. 4519 B. 1831.

Urostigma tsjahela (Burm.f.) Miq. Hook. Lond. Jour. Bot. 6: 567. 1847. (Spelled *Tjakela.*)

U. caulobotryum Miq. Hook. Lond. Jour. Bot. 6: 568. 1847.

U. ceylonense Miq. Hook. Lond. Jour. Bot. 6: 570. 1847. (Misprinted *ceylonnese.*)

U. infectorium Thwaites, Enum. Pl. Zeylaniae 265, in part. 1864.

F. caulobotrya (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 287. 1867. Not Vidal.

Tall tree, much branched, without aerial roots, glabrous; petioles to 7.5 cm. long; blades elliptic tending towards oblong, typically 12.5–19 × 5.5–9 cm., but also 5–9 × 3–5 cm. in a smaller form (examples: 18 × 9 cm., 19 × 8.5 cm., 8 × 5 cm.); base broad, rounded or subcordate; apex slightly narrowed, then abruptly acuminate; acumen thick, about 1 cm. long; upper surface glossy in life, iron- or dark greenish-gray when dried; basal veins similar to the lateral veins; 8–10 sets of conspicuous lateral veins, the upper angle 65° to 75°; only discontinuous tertiary veins; a distinct reticulum and a checkered background; mature receptacles 1–6 on tubercles in the defoliated axils, sessile or short-peduncled, depressed-globose, about 5 mm. in cross diameter when dried, yellowish and dotted when ripe; basal bracts 3, large, almost semicircular, sometimes lobed, the edges loose; male flowers said to have 3 ovate acuminate perianth-parts shorter than the stamen; anther ovate, on a filament of equal length; gall and female flowers with 3–4 perianth-parts; achene obovate, the style long, the stigma cylindric.

TYPE: India: Malabar, Surat.

Distribution: India, especially the west coast and the south; Ceylon; Indo-China.

F. tsjahela sometimes has been confused with the type of *F. lacor* Ham. (formerly known as *F. infectoria* Roxb.). As compared with *F. tsjahela*, *F. lacor* may have aerial roots; and its leaves show a seldom cordate base, a longer slender acumen, distinct basal veins, lateral veins leaving the midrib at a more acute angle, and fewer tertiary veins. Its figs usually are larger, white with a pinkish tinge, sessile, and single or paired in leafy axils. Its distribution includes but extends far beyond that of *F. tsjahela*.

F. geniculata Kurz (For. Fl. Brit. Burma **2**: 447. 1877) resembles *F. tsjahela* closely, but is sometimes pubescent on twigs and fig-peduncles. Its leaf-blades are broader in proportion to their length and show more secondary lateral veins leaving the midrib at a greater angle, and some continuous tertiary veins. Its figs are larger and its male flowers gamophyllous. Its distribution is northeastern India, Burma, Indo-China, and Malaya.

NAMES APPLIED TO THE SPECIES

The prototype of *F. tsjahela* is described as *Tsjakela* on the next-to-last page of the third volume of Rheede's *Hortus indicus malabaricus*. On the last page of that volume under both *Index* and *Errata* the spelling of the name is corrected to *Tsjahela*. The excellent *plate 64* which accompanies the text bears the title *Tsiela*, which had been given previously to *plate 63*. That these illustrations represent different plants is apparent from the contrasting pictures and the vernacular names inscribed on each sheet. The mistake in the plate seems to have misled few people; but the incorrect use of *k* in the text has been followed by almost all writers on the subject, some of whom have introduced other variations: *Tsjakala* by J. Burman (Fl. Mal. 9. 1769) and Graham (Cat. Pl. Bombay 191. 1839), *Tsjakele* by Steudel (Nom. Bot. ed. 2. **1**: 638. 1840), and *Tjakela* by Miquel (Hook. Lond. Jour. Bot. **6**: 567. 1847, and later), King (Ann. Bot. Gard. Calcutta **1**[1]: 57–58, *pl. 70, 84*[x]. 1887; and *in* J. D. Hooker, Fl. Brit. India **5**: 514. 1888), Brandis (Ind. Trees 603. 1906), and others. In this study correct spelling will be used unless it is desired to show the author's orthography.

The pre-Linnean Latin polynomial proposed by Ray as the title of this species was so used by K. Commelin (Fl. Mal. 29. 1696) and was mentioned as a synonym by Stokes (Bot. Mat. Med. **4**: 358. 1812).

N. Burman cited *Tsjahela* Rheede and a species and variety from the herbarium of L. Garcin as synonyms of "*F. tsjakela.*" He characterized the leaves as ovate-oblong, entire and crenate, thus including both Rheede's type and Garcin's variety. No record of crenate leaves seems to have been made by other writers, although the term *undulate* sometimes has been used

In 1789 Aiton described *F. venosa*, an exotic from the East Indies, and cited *Tsjahela* Rheede. The specific name recalls Rheede's statement that the leaves have whitish veins. This title became one of the two most frequently used until King (1887) traced the synonymy and established the priority of the name given by Burman. The authorship of *F. venosa* Ait. sometimes was ascribed to others: to Willdenow by Dennstedt (Schlüss. Hort. Mal. 29. 1818), to the text in Roemer & Schultes (Syst. Veg. 1817) by Blume (Cat. Gew. Buitenzorg 37. 1823), to J. E. Smith by Dillwyn (Rev. Hort. Mal. 13. 1839) and Hasskarl (Nova Acta Akad. Leop.-Carol. **33**: 29. 1867). *F. venosa* Ait. as reported by Voigt (Hort. Sub. Calcuttensis 287. 1845) is *F. lacor* Ham.

Pella ribesioides Gaertn. was proposed as a synonym in Trimen (Handb. Fl. Ceylon **4**: 91. 1898). Gaertner located this genus between *Vaccinium* and *Grossularia*. His plate shows small fruiting bodies clustered on tubercles. A cross section of one body reveals the absence of partitions and the presence of fruits or seeds borne on the inside wall. The vernacular name *Kiripoella*, cited by Gaertner, evidently was the source of the generic name and is almost the same as that in Trimen's text for *F. tsjahela*.

F. infectoria Willd., a name almost as much-used as *F. venosa* Ait., has been a source of great confusion. In 1804 Willdenow (Hort. Berol. fasc. **3**: 36. *pl. 36*) described and illustrated a species of *Ficus* with conspicuously veined leaf-blades. This he asserted to be *F. venosa* Ait. By 1806 he had discovered that he was mistaken; but he retained Aiton's appropriate name for the tree pictured, and re-christened *F. venosa* Ait. as *F. infectoria*, with *Tsjahela* as another synonym. Willdenow's appropriation of *F. venosa* was recognized as illegal by Poiret (Encyc. Suppl. **2**: 654. 1812), who re-named the tree *F. leucantatomá*. This was spelled *leucatoma* by Roemer and Schultes (Syst. Veg. **1**: 501. 1817).

Poiret's mention on p. 657 of *F. venosa* Ait., to which he returned *F. infectoria* Willd., is worth noting because of a reference to it by Hamilton in 1827, and because Poiret included "*Ficus tsjakela* Rheede" as a synonym, as Vahl (Enum. Pl. **2**: 185. 1806) had done.

F. infectoria Willd. often has been confused with *F. infectoria* Roxb. Roxburgh (Hort. Beng. 66. 1814) listed a tree of Bengal as *F. infectoria* (no author). That he believed this to be *F. infectoria* Willd. was shown by his reference to *Tsjahela* Rheede. Later (Fl. Ind. ed. 2, **3**: 551. 1832) he described his Bengal plant as *F. infectoria* Willd., and referred to both *Tsjahela* and *F. tsjahela* Burm.f. However, his description showed that his plant was a new species. When *F. infectoria* Willd. was proved to be an illegal title its specific name, equally illegally, came to be transferred to Roxburgh's tree with Roxburgh's authorship, and has persisted almost to the present time. In recent years *F. lacor* Ham. has been recognized as its

valid title. The following writers have used the name *F. infectoria* Willd., and sometimes its synonyms, for *F. lacor:* Wight (Ic. Pl. **2**: *pl. 665.* 1843), Beddome (Fl. Sylv. India **2**: 222. 1874), Brandis (For. Fl. India 414. 1874), Kurz (above, 446–447), and Trimen (Syst. Cat. Pl. Ceylon 84. 1885).

Wallich's catalog of 1831 listed no. 4519 as *F. venosa* Ait. Subdivisions *A, F. infectoria* Hb. Wight, and *B,* an unamed *Ficus* from Heyne's herbarium are specimens of *F. tsjahela,* according to King (1887). It is disconcerting to find that Wight's specimen belongs here, since his illustration of "*F. infectoria* Willd." is obviously of Roxburgh's species and often is cited as a reference therefor.

Hamilton (Trans. Linn. Soc. **15**: 150. 1827) in an attempt to establish the identity of *Tsjahela* Rheede added another problem. Saying that the plant which he considered was that species did not conform to the description by Willdenow, he described it as *F. venosa,* alluding to Poiret's text (which had cited the author as Aiton), and listing Roxburgh, Burman, and Rheede as references. Most of his characterization applies equally well to both *F. tsjahela* and the variable *F. lacor.* The short petioles and twin figs resemble the latter rather than the former species, but the absence of aerial roots and the maturing of the figs on defoliated twigs point towards *F. tsjahela,* where it has been placed by King (1887). Miquel (Ann. **3**: 286. 1868) and in earlier writings believed that *F. venosa* Ham. was *F. infectoria* Roxb., although he never seemed sure whether or not this species was also that of Willdenow. Haines (Bot. Bihar & Orissa **5**: 832. 1924) has thought that Hamilton's plant might be a form of *F. infectoria* Roxb. or else *F. geniculata* Kurz. In fact, Haines placed *F. tsjahela* close to, if not under, *F. geniculata.*

The synonym *F. indica* Moon was suggested in Trimen's text of 1898 with the note: "not L." I have not seen Moon's book, which includes also *F. bengalensis* L., the accepted name for the ill-defined *F. indica* L.

Miquel (1847) transferred *F. tsjahela* Burm.f. to *Urostigma,* a genus derived from *Ficus* by Gasparrini, describing the species from specimens obtained in southernmost India; and characterized also as new species *U. caulobotryum* from the "East Indies" and *U. ceylonense* from Colombo. The three descriptions differ only slightly. Miquel (Ann. p. 287) returned *U. tsjahela* and *U. caulobotryum* to Ficus. *U. ceylonense* he placed (Ann. pp. 264, 286) under the present *F. lacor,* although he had stated one of its vernacular names to be *Kiripaella.* These three species of *Urostigma,* and *F. caulobotrya,* were allocated to *F. tsjahela* by King. Some mistakes in their names are: *U. caulobotryon* by Dietrich (Syn. Pl. **5**: 554. 1852), *U. caulobotrya* by King (1887) and Gagnepain (in Lecomte, Fl. Gén. Indo-Chine **5**: 761. 1928), *U. ceylonese* by King (1887), *F. caulocarpa* Miq., instead of *F. caulobotrya,* by King (1888).

U. infectorium Thwaites is included in this synonymy because certain numbers of Thwaites' specimens with that name and Miquel as author belong to *F. tsjahela*, according to Trimen (1898).

UNRELATED SPECIES

F. tjiakela Hb. Hook. was allocated by Miquel first to *U. rigidum* Miq. and then to *F. rigida* (Miq.) Miq. Ann. Mus. Bot. Lugd.-Bat. **3**: 286. 1867.

Covellia venosa (Willd.) Miq. is *F. leucantatoma* Poir.

SUMMARY

Ficus tsjahela Burm.f. was named from a pre-Linnean species from the west coast of India. Its name in the original text was misspelled and its illustration was mislabeled. The former mistake, although corrected in the same volume, seems to have passed almost or quite unobserved; the fault in the label was soon noticed.

For nearly 120 years the name proposed by Burman was almost ignored except as a synonym, and the tree usually was called either *F. venosa* Ait. or *F. infectoria* Willd. Both titles were applied also to other plants. The resulting confusion, although not the orthography, was straightened out by King in 1887, and a synonymy prepared. Since that time Burman's seems to have been the only name used.

The preceding study has collected and discussed synonyms listed by King and others, has differentiated *F. tsjahela* from the type of *F. lacor* Ham. and from *F. geniculata* Kurz, and has corrected some mistakes in determination, authorship, and spelling. Herbarium specimens have been examined at the New York Botanical Garden, and literature there and at the Arnold Arboretum, Jamaica Plain, Mass. I am grateful for the use of these facilities and for help given me by those in charge of them.

MONTCLAIR, NEW JERSEY.

BULLETIN OF THE TORREY BOTANICAL CLUB
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TORREYA

EDITORIAL NOTE

With the closing of volume 45 TORREYA ceases to exist as a separate publication. It will be continued as a section in this and subsequent issues of the BULLETIN.

TORREYA originated in a resolution presented at the annual meeting of 8 January 1901. "The space of the BULLETIN being now wholly needed for technical matter," it was resolved "that the publication by the Club of a monthly periodical is desirable, to contain short articles and notes with special reference to the study of the local flora, thus covering the ground occupied by the BULLETIN at its establishment in 1870" (Bull. Torrey Club **28**: 190, 191. 27 Mr 1901). Book reviews also were included, and the *Proceedings of the Club* were transferred to the new periodical in its second year (1902).

In view of the greatly increased costs of publication, it has seemed impracticable to continue to issue a separate periodical for these purposes. It is relevant also that the supply of short articles of the kind contemplated by the founders of TORREYA has been very limited; indeed from the beginning, TORREYA included as many "technical" papers as those "of a popular nature."

For these reasons the Club has voted to merge the two periodicals. The name of the younger, TORREYA, will be preserved at the head of a special section of the BULLETIN, designed to include such materials as: short floristic notes, chiefly of local interest; book reviews; news items; proceedings of the Club. In this way the problem presented in the resolution of 1901 may be solved in a different way.

Somewhat longer papers of a technical nature, such as have often been included in TORREYA, will take their proper places among the papers regularly published in the BULLETIN.— H. W. RICKETT

SHORT ARTICLES AND NOTES

Notes on the Mosses and Lichens of the Great Swamp (New Jersey).[1]

The Great Swamp of New Jersey is located in the southeastern corner of Morris County. Since January 1944 the authors have been conducting an ecological survey of a half-mile-square area in Chatham Township. This area may easily be located, since the northern boundary consists of a road known as Southern Boulevard, which starts at the point where the Public Service Company's power line crosses it and continues west one-half mile. The eastern boundary follows the west side of the power line one-half mile south. Within the area all types of ecological habitats are found. Near the northern boundary are dry sandy soils composed of glacial till and along the southern boundary are soils very acid and rich in peat.

MOSSES

The following mosses we collected in the survey area, the majority of which were

[1] Third contribution to an ecological survey of the Great Swamp.

growing on the higher ground. We are greatly indebted to Miss Frances Wynne of the New York Botanical Garden for determining this material.

Polytrichum piliferum Hedw. 2–IV–44.
Polytrichum commune Hedw. 2–IV–44, 18–IV–44.
Mnium cuspidatum Hedw. 10–IV–44.
Ditrichum pusillum (Hedw.) E. G. B. 10–IV–44, 18–IV–44.
Dicranum bonjeani DeNot. 10–IV–44.
Dicranella heteromalla (Hedw.) Schimp. 18–IV–44.
Heterophyllium haldanianum (Grev.) Kindb. 18–IV–44.
Mnium affine Bland. 18–IV–44.
Eurhynchium strigosum (Hoffm.) B. and S. 18–IV–44.
Pohlia nutans (Schreb.) Lindb. 18–IV–44.

LICHENS

So far we have only collected lichens growing in the grasslands. On the northern end of the survey area, opposite the Chatham Township Public School, is a series of eleven fields running north to south. Growing in these fields we found *Cladonia cristatella* Tuck. and *Cladonia grayii* Nearing. These two species were growing together on gravelly glacial till with a pH of 5.17. Associated with the lichens were grasses and a few herbs. This soil is very poor in plant nutrients as indicated by the very slow invasion of woody plants. On March 11, 1944, the authors denuded a square meter on which *C. cristatella* and *C. grayii* were well established and on June 9, 1945, the quadrat was still barren, in spite of the fact that both species of lichen were growing at the edges of the quadrat.

We are greatly indebted to Mr. William L. Dix of Morrisville, Pennsylvania, for determining the lichen specimens.—WILLIAM F. RAPP, JR., AND JANET L. C. RAPP.

Lippia lanceolata and other Unusual Plants at Cross Lake, New York. On August 25, 1945, while we were returning from a field trip, with a group of graduate students, a short stop on the west shore of Cross Lake in central New York at once yielded a patch of *Lippia lanceolata* Michx., the fog-fruit. It was growing on damp ground near the shore among *Panicum agrostoides* Spreng., *Scirpus americanus* Pers., *Lythrum salicaria* L., and other species in lesser abundance. The very unfavorable weather prevented stopping longer to make a more extensive study of the area at that time.

The manuals state the range of *Lippia lanceolata* as New Jersey to southern Ontario and Minnesota and southward to Texas and Florida. Actual records of its occurrence between southern New Jersey and Michigan seem to be rare. House[1] does not list *Lippia lanceolata* from New York State. Because the Cross Lake station appears to be isolated at some distance from the nearest recorded stations in New Jersey, Ohio and Michigan, another trip was made to ascertain the abundance and range of Lippia in that area.

On September 5, accompanied by Dr. R. T. Clausen and Miss Gertrude Miller we visited Cross Lake again, spending most of the day exploring much of its shoreline vegetation as well as dredging from boats for aquatic species. This survey revealed that *Lippia lanceolata* is rather generally distributed in low wet ground along much of the eastern and western shores of the lake and also along the Seneca river

[1] House, H. D. Flora of New York. N. Y. State Mus. Bull. 254. 1924.

where it leaves the lake. In several places *Lippia* forms dense mats covering extensive areas near shore. None was found more than 300 feet from the water's edge. Most of the plants were sterile but a number of flowering and fruiting plants were observed on the higher places back from shore. The plants were mostly decumbent, or with erect branches when crowded, rather than prostrate or creeping as they so often occur in the southern states.

Cross Lake is partly in Cayuga county and partly in Onondaga county. It is about 5 miles long. Its elevation is 375 feet above sea level according to the U. S. Topographic Survey map. Its south end is traversed by the Seneca river which here is canalized and used by the Barge Canal. Most of the shore and much of the bottom of the northern part of the lake is composed of soft marl and broken shells.

The following plants rarely found in central or western New York, were also collected in or around Cross Lake on August 25 or September 5, 1945.

PANICUM AGROSTOIDES Spreng. Common on wet shores along Cross Lake and the north shore of the Seneca river where it leaves the lake; in Cayuga and Onondaga counties.

ACNIDA CANNABINA L. On muddy banks of the Seneca river just west of the lake; Onondaga county.

AZOLLA CAROLINIANA Willd. Floating among *Lemna minor* L. in a sluggish inlet entering the lake through a bog near the northwest corner; Cayuga county.

NAJAS MINOR Allioni. In shallow water near shore and also dredged in deeper water in several places off the east shore of the lake; Cayuga county.

The occurrence of this heterogeneous assemblage of plants, otherwise unknown or known from but few stations in central or western New York, is a subject for speculation. How did they arrive in Cross Lake and why did they become established there? Or are some of them indigenous there? Probably no one answer will suffice for all of the five species mentioned. However, the fact that Cross Lake is a mecca for fisherman and is traversed by much water traffic between Lake Erie and the Hudson River must not be overlooked in searching for explanations for the appearance of these plants in Cross Lake. The non-acid soil along most of the shore line and a rather constant and controlled water level during the summer months may furnish here a more favorable habitat for these species than occurs elsewhere in western New York.

Specimens of all the species mentioned have been collected by us and have been deposited in the herbarium of the Department of Botany at Cornell University.—W. C. MUENSCHER AND BABETTE I. BROWN.

PROCEEDINGS OF THE CLUB

Minutes of the Meeting of May 16, 1945. The meeting was called to order by President Seaver at 3: 30 p.m. at The New York Botanical Garden with fourteen members and friends present. The minutes of the preceding meeting were approved as read.

The secretary read the report (attached to these minutes) of the committee appointed to compose a congratulatory message to The New York Botanical Garden. The report was accepted as read. Dr. Karling reported that the message was to be engraved by the Columbia University Press.

The president read an invitation from the Biological Laboratory of Fordham University to the Club to attend the ceremony, on May 24th, conferring the honorary degree of Doctor of Science upon Dr. William J. Robbins.

Dr. J. T. Baldwin, Blandy Experimental Farm, Boyce, Va., was elected to life membership in the Club. One annual member and one associate member were also elected.

Dr. Karling made a motion requesting affiliation of the Torrey Botanical Club with the Union of American Biological Societies. Dr. Cronquist seconded the motion. There was some discussion concerning the advantages and obligations attendant upon such an affiliation. The motion was carried unanimously.

Miss Hanson raised the question of granting a discount on subscriptions on back sets of the BULLETIN to book-sellers or agencies. Dr. Karling moved the appointment by the president of a committee of three: the editor, the business manager, and the treasurer, to investigate this question and decide upon a policy. Dr. Levine seconded the motion and it was carried.

The business meeting adjourned at 4:00 p.m. to the lecture hall for an interesting and instructive program by Dr. A. B. Stout on "Types of Intra-specific Incompatibilities."

The speaker's abstract follows:

In respect to the locus of sexual reproduction in the life cycle and to the scope, action, and genetics of the modifying factors of incompatibilities, there are three distinctive main classes of incompatibilities which may be designated as follows:

I. *The diplont-haplont class.* In the flowering plants the inhibiting effects of self- and cross-incompatibilities occur chiefly during reactions between the diploid tissues of the pistils of flowers of the sporophytic generation and the haploid pollen tubes of the alternating gametophytic generation.

II. *The haplont-haplont class.* In the fungi the reactions of incompatibilities occur in the interrelations between individuals that are haploid, bisexual and gametophytic.

III. *The diplont-diplont class.* In the ciliates among animals the reactions of incompatibilities operate chiefly in the relations of selective conjugation between individuals that are bisexual and diploid and hence comparable to the sporophytic generation in plants.

The incompatibilities noted in this presentation are selective limitations to the sexual reproduction of homomorphic hermaphrodites. They limit or prevent both self-reproduction and intra-genotypic cross-reproduction. They effect inter-genotypic intra-specific reproduction.

Incompatibilities operate by inhibiting certain of the physiological interactions that are essential to sexual reproduction but which are not features of nuclear or gametic sexuality.

Pollen-tube reactions in the pistils of flowering plants, fusions of mycelia and spermatial fertilizations in fungi, and conjugations between individuals of ciliates are all stabilized reactions of intraspecific sexual reproduction. When there are no incompatibilities there is unrestricted interaction in these features of intraspecific reproduction. Incompatibilities are superimposed on these mechanisms and they effect certain failures in interactions which would otherwise occur.

Incompatibilities are genetically determined by factors which segregate in meiosis. In the homomorphic bisexual members of a population they may be the only feature of sexuality that does segregate in meiosis. This situation has not been recognized in many considerations of sexuality especially in the fungi.

The simplest mode of incompatibilities is that which is determined by a single allelic pair of factors (personate mode) operating in haplont-haplont relations. Then there may be only two mating groups. A minimum number of multiple alleles in a haplont-haplont relation is three. In all the classes there may be numerous multiple factors and numerous mating genotypes. Further complexities involve two or more allelic series (a) of incompatibility factors (amphipersonate) or (b) of one such series in complementary relations with factors which favor fertility (associate mode) or of more than one series of each (amphiassociate).

The basic incompatibility reaction is evidently one of independent self-antagonism. But the presence of two or more different factors enforces various types of complementary and competitive reactions.

In addition to incompatibilities there are other methods of preventing self- and intra-genotypic reproduction and of enforcing bigenotypic reproduction in hermaphrodites. (a) There are herkogamy and dichogamy which operate to separate elements of sexual reproduction previous to their interaction. (b) There are the conditions of polymorphism, especially developed in dimorphic and trimorphic species of flowering plants, in which incompatible reactions are correlated with morphological features.

It is of course to be recognized that in any truly dioecious species the reproduction of the unisexual individuals is obligated bigenotypic.

Intraspecific incompatibilities operate with remarkable similarity in phanerogams, in fungi, and in ciliates. Differences in the locus of sexual reproduction in the life cycles of these diverse and phylogenetically widely separated groups of organisms are reflected in three distinct classes of expression and genetic control which may be designated (I) haplont-diplont, (II) haplont-haplont, and (III) diplont-diplont. Without doubt future studies in the groups mentioned and in other groups of plants and animals that were not mentioned will reveal further modes or even other classes of reaction and determination.

After the scientific program the members were served tea by the Garden Staff in the Members' Room.

Respectfully submitted,
FRANCES E. WYNNE,
Recording Secretary

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